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REVISION OF THE GENUS *MYRMOTERAS* (HYMENOPTERA: FORMICIDAE)

MARK W. MOFFETT[1]

ABSTRACT. The Asiatic formicine ant genus *Myrmoteras* is revised in full, with descriptions of ten new species and redescriptions of the eight previously described species here considered valid; *M. kemneri* is provisionally synonymized with *M. barbouri*. Among the new species are the first records of *Myrmoteras* from India and Sulawesi.

Two subgenera are recognized: in the subgenus *Myrmoteras* (with seven species in two species-groups) a pair of long trigger hairs extends from the labrum; in the new subgenus *Myagroteras* (with eleven species in four species-groups) the trigger hairs are absent. Cladistic analysis supports the informal species-group divisions and (if it is assumed that loss of palpal segments is more probable than regain) the monophyly of both subgenera.

INTRODUCTION

The tribe Myrmoteratini, containing the single genus *Myrmoteras*, is a small group of infrequently collected formicine ants with a distribution restricted to tropical Asia. With their oddly shaped heads, huge eyes, and extraordinarily long mandibles, *Myrmoteras* are unquestionably among the most bizarre ants in the world fauna.

Myrmoteras has been regarded as relatively primitive since Emery (1925). Characters considered ancestral for the Formicinae include the asepalous proventriculus (Eisner, 1957) and the wing venation (Brown and Nutting, 1949). Obviously derived characters are numerous, however, and include the most conspicuous and distinctive morphological features. Notable here is the elongation of the mandibles, which are linear with approximate insertions. The back of the head has become widened, apparently to accommodate relatively massive mandibular muscles, and a distinctive occipital lobe has formed. In addition, there has been the development, in some species, of trigger hairs extending from the labrum forward between the mandibles.

These morphological characters relate in large part to a specialized mode of foraging behavior. *Myrmoteras* workers and queens are capable of opening their mandibles about 280°, wider than has been observed for any other ant (Figs. 1, 2). In *M. toro*, a species I have observed in Sulawesi, workers seize active, soft-bodied prey by snapping their mandibles forward from the fully open position. This is essentially the same prey capture technique as that used by ants in other subfamilies of the Formicidae: odontomachine ants (Ponerinae) and dacetine ants (Myrmicinae). All three groups depend heavily or entirely on the capture of large or agile prey by solitary foragers, without the benefit of recruitment.[2] In addition, R. W. Taylor (CSIRO, Canberra, Australia) has discovered several species of Leptanillinae which are also trap-jaw ants.

The constellation of anatomical and behavioral characters that bear on trap-jaw predation are apparently apomorphies in the respective subfamilies of each group

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[2] In certain trap-jaw species the trap-jaw apparatus has been modified secondarily to serve more effectively for defense (Carlin, 1983). This has not occurred in *Myrmoteras* species.

containing trap-jaw ants. That these traits have recurrently coevolved suggests that they represent an 'adaptive syndrome,' in other words, a suite of characters likely to evolve together or in some sequence to produce a more or less narrowly defined phenotype with specific functions (in this case the trap-jaw apparatus). The prevalence of odontomachine and dacetine ants in tropical ecosystems around the globe attests to the widespread significance of the niche open to ants that have convergently developed trap-jaw predation. Indeed, *Myrmoteras* ants are probably more ecologically important in tropical Asia than the infrequency with which they have been collected suggests: those localities at which collecting has been most intense in recent years, such as Gunung Mulu National Park, are now known to harbor several species.

RELATIONSHIPS

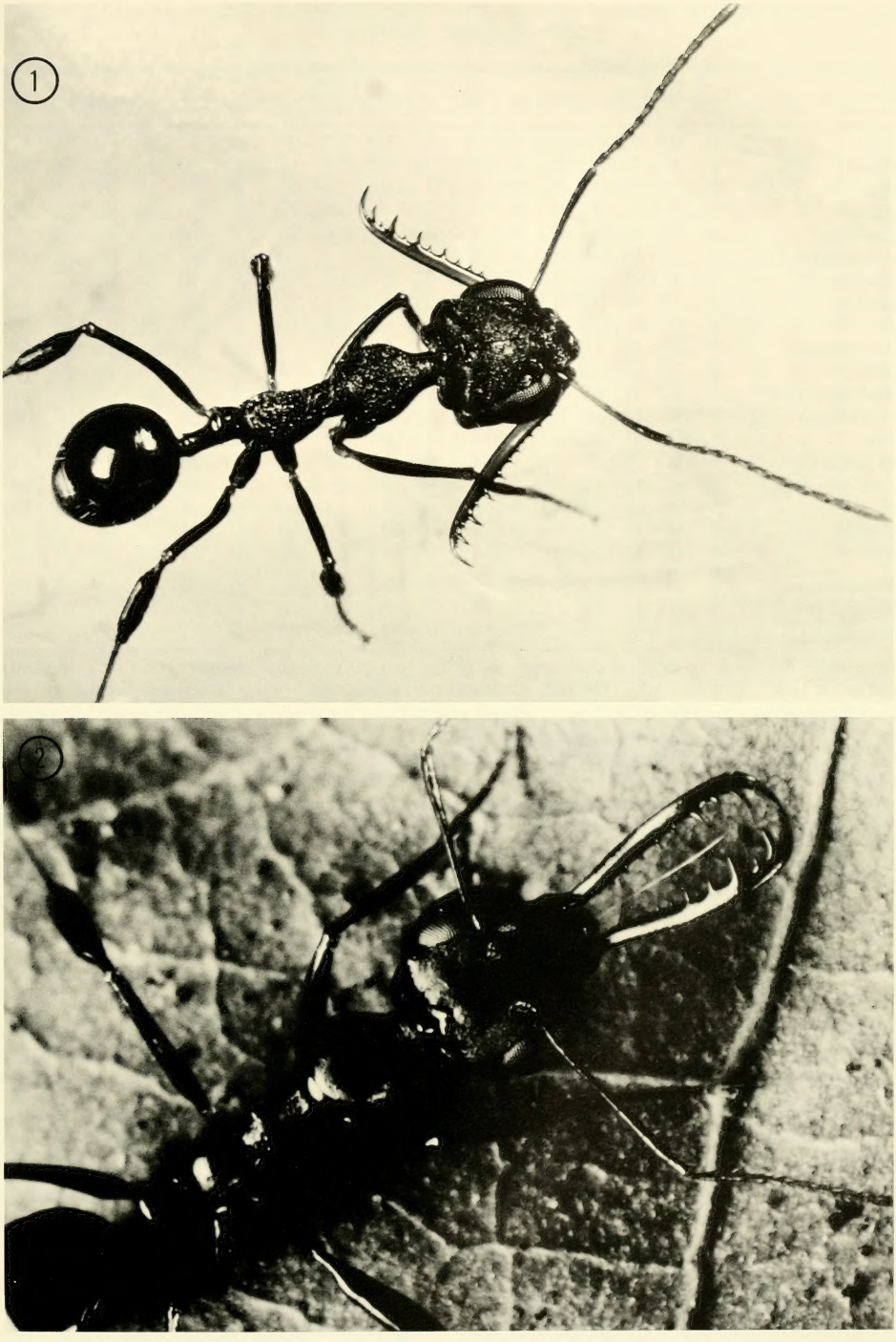
The species of *Myrmoteras* fall into two distinct groups, one of seven species (subgenus *Myrmoteras*) and one of eleven (subgenus *Myagroteras*) which can be readily distinguished by labral characters. Females in the subgenus *Myrmoteras* have a pair of prominent trigger hairs that originate from the middle of the dorsal face of the labrum. The species of *Myagroteras* lack long, prominent trigger hairs (although there are two much shorter and more widely separated labral hairs), and the dorsal surface of the labrum is more or less rounded, not coming to a distinct medial point. Although not noted by previous authors, these characters are easily recognized even in the field, and are apparent in illustrations of head structure in previous taxonomic treatments of *Myrmoteras*, for example in plate 6 of Creighton (1930). Another conspicuous character distinguishing *Myagroteras* from *Myrmoteras* is the presence of a longitudinal sulcus extending between the frontal area and medial ocellus in all *Myagroteras* species except *M. insulcatum*. In the subgenus *Myrmoteras* the sulcus is invariably very feeble or absent. Gregg (1956) indicated that *Myrmoteras* species could be divided into two groups based on this feature.

The two groups also differ in the degree to which the mandibular shafts are bent ventrad approximately at the position of the penultimate tooth. In *Myrmoteras* the mandibles are strongly bent, so that there is a distinct angle visible in lateral view. *Myagroteras* ants have only a very slight bend or downward curvature at the same position.

The behavior of *Myagroteras* species has not been studied. However, it seems reasonable to assume that the presence or absence of trigger hairs must bear directly on differences in foraging behavior between the two groups, and therefore probably is a reflection of significant ecological differences. This, and the ease with which the two groups can be distinguished, suggests that formal division of the genus would be of heuristic value. A cladistic study of *Myrmoteras* with the aid of the program PAUP (version 2.3), written by David L. Swofford, has clarified the phylogeny of the genus and allowed for an evaluation of whether such a division is justified. This study suggests, but does not unequivocally support, formal division of *Myrmoteras*. Monophyly of both groups is supported if it is assumed that loss of palpal segments and of a well-demarcated frontal area is more probable than regain.

Character Coding for Computer Analysis

The characters used in the analysis are given in Table 1. Definitions of all characters are given in the section on terminology. Characters 19 and 21 (cephalic sculpture and occipital lobe sculpture) were treated as unordered; all other characters were binary or ordered. The characters were allowed free reversibility as in Wagner parsimony (Felsenstein, 1982; Farris, 1970). As discussed below, however, losses were considered more probable than gains for certain characters, a



Figures 1–2. Live workers of the genus *Myrmoteras*. 1. *M. toro* paratype (subgenus *Myagroteras*). 2. *M. barbouri* forager from Singapore (subgenus *Myrmoteras*; trigger hairs barely discernible).

TABLE 1. DATA MATRIX OF MORPHOLOGICAL CHARACTERISTICS FOR SPECIES OF *MYRMOTERAS* AND ONE HYPOTHETICAL OUTGROUP.†

Taxon	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Outgroup	0	0	0	0	?	?	?	?	0	?	0	0	?	?	0	0	?	?
M. barbouri	1	1	0	0	0	0	P	0	0	P	1	1	0	0	1	0	0	0
M. binghami	1	1	0	0	0	0	0	1	0	P	0	0	0	0	P	0	0	0
M. iriodum	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0
M. mjoebergi	1	1	0	0	0	0	1	0	0	0	2	1	0	0	1	0	0	0
M. brachygnathum	1	1	0	0	0	0	0	0	0	1	2	1	0	1	1	P	0	P
M. ceylonicum	1	1	0	0	0	0	0	0	0	1	0	0	0	1	P	P	0	P
M. scabrum	1	1	0	0	0	0	0	0	0	1	2	2	P	P	0	P	0	P
M. bakeri	0	0	1	1	1	P	1	0	0	1	1	1	1	1	1	1	0	1
M. diastematum	0	0	1	1	P	1	1	0	P	1	1	0–1	1	1	1	1	0	1
M. indicum	0	0	1	1	1	0	1	P	1	1	2–3	1	1	1	P	1	0	P
M. chondrogastrum	0	0	1	1	1	P	1	0	1	1	1	0	1	1	1	1	0	P
M. donisthorpei	0	0	1	1	P	0	1	0	0	1	1	0–1	1	1	P	P	0	P
M. karnyi	0	0	1	1	?	?	1	1	0	?	?	?	1	1	?	?	0	?
M. insulcatum	0	0	0	1	1	1	2	0	0	1	3	1	0	0	P	P	0	1
M. morowali	0	0	1	1	1	1	1	0	0	1	0	0	1	1	0	P	1	P
M. toro	0	0	1	1	P	0	1	0	0	1	0	0	1	1	P	P	1	P
M. williamsi	0	0	1	1	1	0	1	0	0	1	0	0	1	P	P	P	1	P
M. wolasi	0	0	1	1	1	0	1	0	0	1	0	0	1	1	0	P	1	P
Sg. Myrmoteras	1	1	0	0	0	0	?	0	0	?	0	0	0	?	0	0	0	0
Donisthorpei-group	0	0	1	1	1	0	1	?	?	1	1	0	1	1	?	1	0	?
Williamsi-group	0	0	1	1	1	0	1	0	0	1	0	0	1	1	0	?	1	?

† In the table "?" refers to missing data and "P" refers to a polymorphic condition, or an intermediate or ambiguous condition, as discussed in the text. Character numbers refer to the following characters: 1. trigger hairs; 2. labrum shape; 3. frontal sulcus; 4. apical mandibular bend; 5. mandibular angle; 6. mandibular grooves; 7. tooth counts; 8. preapical denticle number; 9. apical denticle number; 10. apical denticle size; 11. maxillary palps; 12. labral palps; 13. lateral clypeal flanges; 14. clypeal convexity; 15. frontal area; 16. orbital grooves; 17. postocular distance; 18. rugae above antennal bases; 19. cephalic sculpture (unordered character); 20. clypeal sculpture; 21. occipital lobe sculpture (unordered character); 22. metathoracic tubercle ruga; 23. propodeal shape; 24. metanotal groove; 25. iridescence; 26. petiolar rugae; 27. density of pilosity; 28. height of pilosity; 29. metathoracic tubercle hairs; 30. sternum of petiole; 31. propodeal declivity; 32. HW, character 1; 33. HW, character 2; 34. CI; 35. ML, character 1; 36. ML, character 2; 37. SI; 38. EI; 39. OLI; 40. TWI; 41. HFL. The final three rows of data in the table are characters for the hypothetical ancestral species of the subgenus *Myrmoteras* and the *donisthorpei* and *williamsi* species groups.

possibility not allowed for in the PAUP program.

When a character showed polymorphism within a species (i.e., the presence of mandible grooves in *M. bakeri*) it was coded as if the data were missing for that species. Species represented by single specimens were treated as polymorphic for a character if the specimen showed a borderline condition. Range limits for numerical characters were chosen to separate cleanly the maximum number of species. For several of the numerical characters (SI, HFL, TWI), species showing any overlap with the range in values between an upper and a lower limit were coded as if the data were missing; only those consistently higher than the upper limit or lower than the lower limit were assigned character states. As a result, only species demonstrating extreme differences in these characters were contrasted. This was done because the limited material available for most species is certainly not sufficient to show much of the intraspecific variation actually present. Finally, for certain characters (ocular groove, rugae above antennal bases, mandibular angle, frontal area, propodeal shape) in which the character states were judged

TABLE 1. EXTENDED.

Character																						
19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	?
1	0	0	0	P	P	1	0	0	1	0	0	1	1	P	1	1	0	1	P	1	P	1
3	1	0	0	P	0	1	0	P	1	0	0	1	1	1	1	1	0	1	1	1	P	1
2	1	0	P	0	0	1	0	P	1	0	0	1	1	1	1	1	P	1	1	1	0	1
2	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	1
2	1	0	0	1	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	P
1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	P
0	1	1	0	P	0	0	1	0	0	0	0	0	1	1	0	0	0	P	0	0	0	1
2	1	0	0	0	P	0	0	0	1	0	0	1	0	0	1	1	1	P	1	P	1	0
2	1	0	1	0	1	0	0	1	0	0	0	1	1	0	1	1	1	1	1	P	0	P
2	1	0	1	1	1	0	0	0	1	P	0	1	P	0	1	1	P	P	P	P	0	P
1	0	0	1	0	1	0	0	0	1	0	1	1	1	0	1	1	1	1	1	P	0	P
1	0	0	1	0	1	0	0	0	1	0	1	1	0	0	1	1	1	P	1	P	1	0
?	?	?	?	1	?	?	?	?	?	?	1	?	?	0	1	?	?	?	1	?	0	?
2	1	0	P	P	P	0	0	P	1	0	0	1	1	0	1	1	1	P	0	0	P	P
1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	P	P	P	0	P	0
0	1	2	0	P	0	0	0	1	1	0	0	1	1	0	1	1	1	P	0	1	P	P
1	0	1	0	1	1	0	0	0	1	P	0	1	1	0	1	1	1	P	0	P	P	P
0	0	2	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	P	1	P	P	P
1	1	0	0	0	0	?	0	0	1	?	0	1	1	0	?	?	0	?	1	?	0	1
0	0	0	1	?	1	0	0	0	1	0	1	1	?	0	1	1	1	1	1	?	?	0
0	0	1	0	?	?	0	0	?	1	0	0	1	?	0	1	1	1	?	0	?	?	0

qualitatively, species in which there was an intermediate condition were treated as if the data were missing, because of difficulties in consistently assigning character states.

OUTGROUPS

The genus most closely related to *Myrmoteras* appears to be *Gesomyrmex* (specimens of *Santschiella*, an African genus possibly close to tropical Asian *Gesomyrmex*, were not available for study). *Gesomyrmex* females have very large eyes (in minors EI ranges from 79 to 93), and the shape of the eyes is similar to that of *Myrmoteras*. In addition, the petioles of most *Gesomyrmex* minors have a pair of ventral hairs at the base of both the anterior and posterior peduncles, as is the case with *Myrmoteras*. Monophyly of *Gesomyrmex* is evidenced by the position of the antennal bases, the eight-merous antennae, and other characters.

The mandibles of *Gesomyrmex* minors come closest within the Formicinae to resembling those of *Myrmoteras* females. The mandibles are long (MI 49 to 54, or greater if the forward projection of the clypeus is excluded), and, unlike other Formicinae outside of *Myrmoteras*, the toothed margin of the mandible runs virtually parallel with the lateral margins (so that the blade is linear rather than subtriangular). Moreover, the two teeth proximad to the apical tooth are shorter than the teeth to either side of them, and in many cases are reduced in size to a degree almost comparable to the apical denticles of *Myrmoteras* (some specimens of Australian genus *Myrmecorhynchus* also approach this condition). In addition, most *Gesomyrmex* minors have the mandibles relatively strongly curved ventrad at about the same position as the strong apical mandible bend characteristic of the subgenus *Myrmoteras*. Thus, the mandibles of many *Gesomyrmex* minors seem to be approaching the condition characteristic of *Myrmoteras*.

The proventriculus of *Gesomyrmex* is

sepalous, which is the derived condition for Formicinae (Eisner, 1957). In contrast, the proventriculus of *Myrmoteras* lacks sepals. The anatomy of the *Myrmoteras* proventriculus is unusual, however, and not well understood (Eisner, 1957). The asepalous condition of the proventriculus in *Myrmoteras* does not preclude a close relationship to *Gesomyrmex*, although further comparative studies using proventricular structure and other characters will be necessary to clarify the phylogenetic relationships of these and other formicine genera.

Character Polarity

Comparison of *Myrmoteras* with *Gesomyrmex*, *Myrmecorhynchus*, and other Formicinae indicates that several characters found to vary within *Myrmoteras* can be polarized for cladistic analysis. *Gesomyrmex* and *Myrmecorhynchus* show at most a trace of the frontal sulcus; the presence of a well-defined sulcus is therefore considered synapomorphic within the genus *Myrmoteras*, as is the lack of a distinct apical mandible bend.

In all other formicines examined the labrum either lacks a distinct dorsalmost surface, or this surface is narrow and truncate. In genera such as *Gigantiops*, *Opisthopsis*, *Camponotus*, and *Formica* the (often numerous) labral hairs are short to moderately long (but apparently never longer than the length of the labrum; see Gotwald, 1969). By contrast, in the genera *Oecophylla* (Gotwald, 1973), *Myrmecorhynchus*, and *Gesomyrmex* the labrum has one or two pairs of hairs which are much longer than any other labral pilosity. These hairs are very slender and originate far apart on the labrum, and thus resemble those of *Myagroteras*. The hairs either project back over the mouthparts, or more or less forwards, beneath the mandibles. In *Gesomyrmex* there is often only a single pair of long, widely separated hairs, and in some species these hairs are almost as long as the mandibles. These observations support the view that the trigger hairs and projecting labrum of species in subgenus *Myrmoteras* represent synapomorphies.

Well-developed ocular grooves, the presence of a slight iridescent sheen, and the strongly dilated condition of the middle and hind tibiae are characters apparently unique to certain species of this genus, and these character states are therefore considered synapomorphies. The 6,4 palpal formula and presence of a well-defined frontal area were treated as plesiomorphies.

Cladistic Analysis

In the initial runs of the complete data set I used global branch swapping with MULPARS (search for multiple minimum length trees). Unfortunately, the PAUP program does not allow for irreversible conditions: I consider the loss of palpal segments and complete loss of a well-demarcated frontal area to be much more probable than regain. The initial run resulted in trees where reversals in the loss of these characters occurred. At this point an attempt was made to find more parsimonious trees by reducing the likelihood of reversals.

Several of the reversals present in the trees from the initial run occurred within clusters of species. These species clusters consistently resolved regardless of whether palpal and frontal area characters were used in the analysis; there were also characters supporting the monophyly of each of these clusters. Therefore, each cluster was collapsed to a single, hypothetical ancestor species, with the assumption that any of the tree configurations found during runs with or without palpal and frontal area characters could represent the actual phylogeny of the cluster. The clusters involved were the *ceylonicum* and *binghami* species groups, which were further collapsed to a single taxon, and the *donisthorpei* group; this reduced the number of taxa to ten. The character states assigned to the ancestral species for each group were deduced through consider-

ations of parsimony using the algorithm of Maddison *et al.* (1984), except for the following characters: maxillary palpal segmentation, labral palpal segmentation, and frontal area. Since losses for these characters are considered essentially irreversible, the highest number of palpal segments and best-developed condition of the frontal area within each group were treated as the ancestral condition for that group.

The *williamsi* group was consistently resolved in the six most parsimonious trees found for this modified data set. The number of taxa under consideration could then be further reduced by collapsing the *williamsi* group to a single ancestral taxon. With the number of taxa reduced to seven it became possible to carry out an exhaustive search for the most parsimonious trees. The three resulting trees are given in Figure 3 (trees A–C), along with the basic structure of the majority of trees from the initial run (tree D).

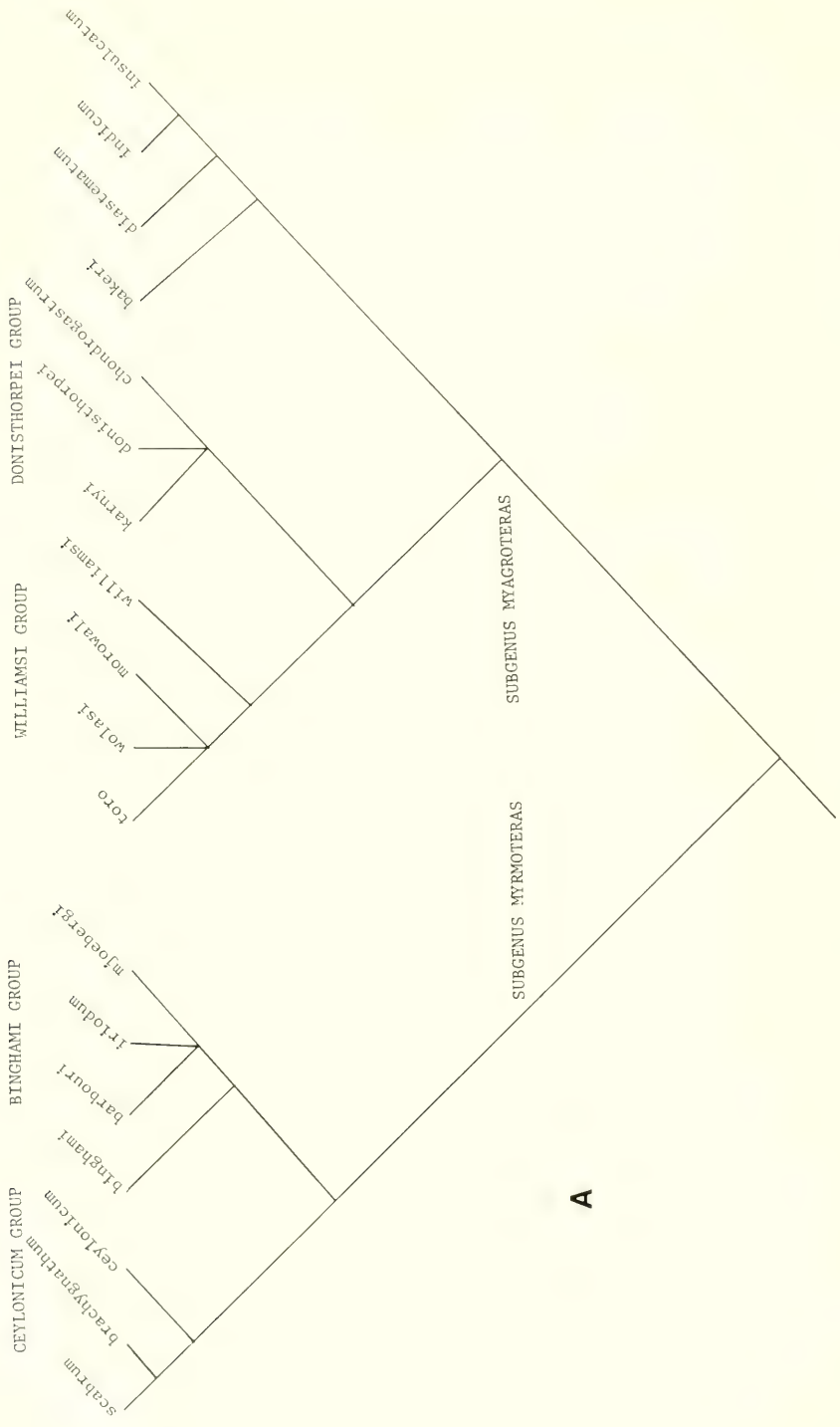
RESULTS

Inclusion of the complete data matrix consistently results in the placement of the subgenus *Myrmoteras* as the sister group to the species *M. insulcatum* within the *Myagroteras* tree. However, when the initial data set is considered without palpal and frontal area characters, *Myrmoteras* and *Myagroteras* resolve as monophyletic sister taxa. Monophyly of both groups is also realized when the occurrence of regains in palpal and frontal area characters is constrained by first collapsing species groups as discussed in the previous section. The three trees resulting from this procedure contain 101 steps (including changes within the collapsed groups), five more than the most parsimonious trees found when no restrictions were made on reversals in palpal segment and frontal area loss. Of these, tree A (Fig. 3) is considered most reasonable because it assumes one event of palpal segment and frontal area regain, rather than two. I have chosen to accept this tree, and therefore the monophyly of both groups, because trees in which the subgenus *Myagroteras* is paraphyletic (for example, Fig. 3, tree D) are less parsimonious given my initial assumptions on character evolution. This is true even after the number of reversals in the palpal and frontal area characters is reduced by manually recoding transitions between character states on these trees. Monophyly of *Myagroteras* is supported by the frontal sulcus and mandibular bend characters (although the results do not change if the mandibular bend character is not polarized). (Monophyly of *Myrmoteras* is supported by the labral shape and pilosity [trigger hair] characters.)

In the subgenus *Myrmoteras*, the *ceylonicum* and *binghami* groups consistently resolved as monophyletic sister groups. *M. ceylonicum* is the sister taxon to the other species in the *ceylonicum* group. *M. barbouri, iriodum,* and *mjoebergi* form a clade within the *binghami* group, although the relationship between these species is unclear.

The structure of the *Myagroteras* tree is less certain. The species *M. williamsi* is most likely the sister taxon to other species in the *williamsi* group, but if palpal segment characters are deleted from consideration, the species sorts out at the base of the *donisthorpei* clade near *M. karnyi.* Although the *donisthorpei* group was consistently resolved as monophyletic, placement of *M. karnyi* in this group is problematic because the type (and only known specimen) of this species was not located. The possibility remains that *M. karnyi* is actually closer to *M. williamsi.* Placement of *M. karnyi* in the *donisthorpei* group was a result of coding for probable similarities in petiolar shape and sculpture based on the original description (Gregg, 1954).

The position of the species *M. insulcatum* in the tree is unclear. This ant represents either the sister taxon to other *Myagroteras* species (as in Fig. 3, tree C), or is derived from the *M. bakeri* group (Fig.


insulicatum
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williamsi
motowali
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irtodum
bartoburi
binghami
ceylonicum
brachygnathum
scabrum
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BINGHAMI GROUP
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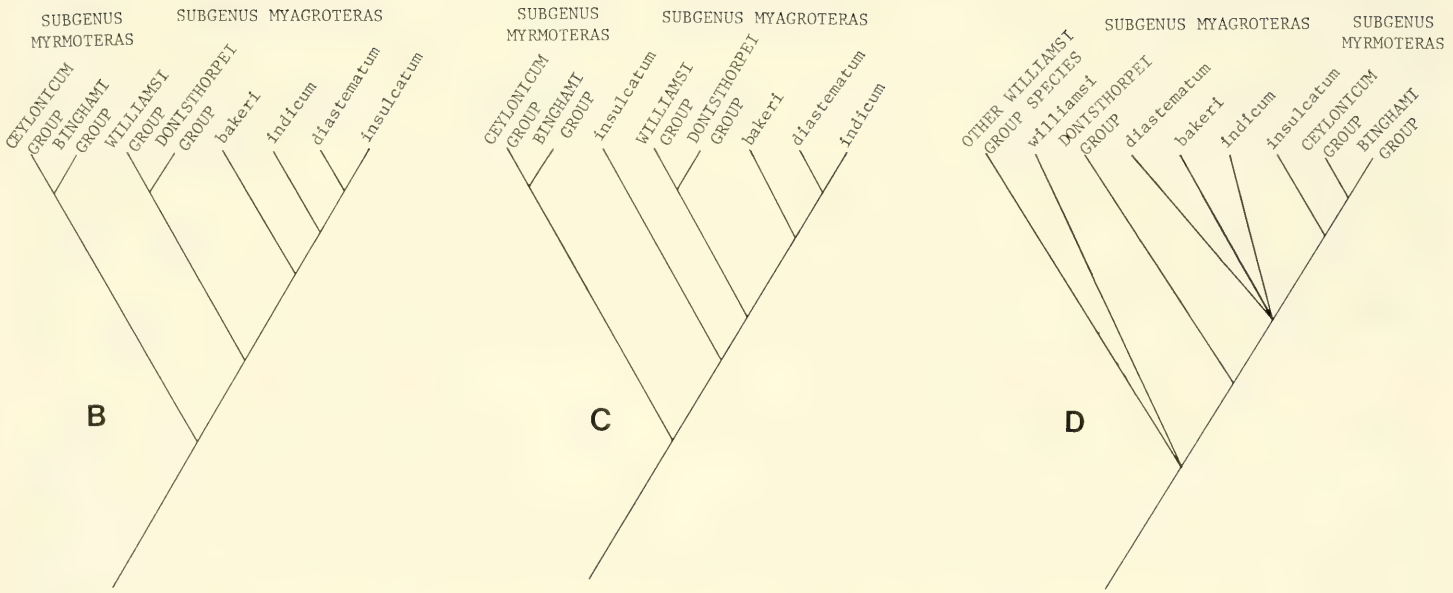


Figure 3. Alternate cladograms of the genus *Myrmoteras*. Trees A–C result from the assumption that reversal of palpal segment or frontal area loss is unlikely (see text for methods used). Tree D shows the structure common to most of the equally parsimonious trees obtained when loss and gain of the same characters were treated as equally likely. Nodes with more than two branches indicate unresolved relationships. Only tree A is presented in its entirety; in the other trees the positions of monophyletic species groups are indicated.

3, trees A and B). Given the latter hypothesis, and presuming *Myagroteras* is monophyletic, the character states this species uniquely shares with subgenus *Myrmoteras* (such as in clypeal shape and lack of the frontal sulcus) must represent homoplasies.

The adequacy of the phylogeny supported here will become clearer when additional material from the genus is available, as future collections of *Myrmoteras* will certainly continue to yield a high proportion of new species, and should also greatly clarify intraspecific variation.

TERMINOLOGY AND CHARACTER STATES

Below I define the measurements, indices, and special descriptive terms used in this revision. In cases where the character in question was used in the cladistic analysis, the individual character states are also defined, with the coding for each state used in cladistic analysis given in brackets. Unless otherwise indicated, the characters were treated as an ordered sequence of states. Character states coded as [?] were treated as absent data (see previous section).

Precise measurements are necessary to determine subtle differences in body proportions that often distinguish species. Measurements were made with an ocular micrometer on a Leitz microscope, to a precision of at least 0.01 mm, except measurements of trunk length, which are precise to an estimated 0.03 mm. All measurements are given to the nearest 0.01 mm; indices such as CI were calculated before converting micrometer units to millimeters. Sculpturing terminology follows that of Harris (1979). Scanning electron micrographs were prepared with an AMR 1000a SEM, using gold-palladium coated specimens.

General Characters

Iridescence. Refers to presence of a fine iridescent sheen on the head and trunk. **Character states**: [0] no iridescence (although body surface often lustrous); or [1] feebly iridescent.

Pilosity. Generally refers to the long, conspicuous erect to suberect hairs on the head and body.

Height. Typical height of longer hairs on trunk. **Character states**: hairs [0] long (height at least 0.18 mm); or [1] short (height < 0.15 mm).

Density. Estimated for workers by counting hairs breaking dorsal margin of trunk viewed in profile, excluding hairs arising from metathoracic tubercles. **Character states**: pilosity [0] sparse (less than 10 hairs) to moderate (10 to 29 hairs); or [1] dense (30 to 39 hairs) to very dense (40 hairs or more).

TL (*Total length*). Sum of ML + HL + WL + petiole length + gaster length. Sizes small (less than 5.0 mm), medium (5.0 to 6.0 mm), or large (greater than 6.0 mm).

Characters on Head (Excluding Mandibles)

CI (*Cephalic index*). 100 × HW/HL. **Character states**: head [0] narrow (CI at most 108); or [1] broad (CI > 108).

Cephalic sculpture. **Character states** (unordered character): dorsum of head (excluding clypeus) is [0] conspicuously rugose; [1] granulate; [2] smooth (excluding fine, feeble rugae between antennal bases); or [3] punctate.

Clypeal sculpture. **Character states**: clypeus [0] granulate or granulo-rugose; or [1] lacking granulate sculpture.

Clypeus, convexity. **Character states**: clypeus [0] feebly convex medially; [?] intermediate condition; or [1] strongly convex medially.

Clypeus, lateral flanges. **Character states**: lateral flanges [0] relatively poorly defined; [?] intermediate condition; or [1] well-defined because of relatively abrupt shift in plane relative to raised medial region.

EI (*Eye index*). 100 × EL/HW. **Charac-**

Figures 4–5. Labral structure in an oblique anterior-dorsal view. 4. Labrum of *M. indicum* (subgenus *Myagroteras*); the arrow indicates one of the long labral hairs. 5. Labrum of *M. mjoebergi* (subgenus *Myrmoteras*).

Scale lines. 0.05 mm.

ter states: [0] EI at most 60; or [1] EI > 60.

EL (*Eye length*). The maximum diameter of the eye.

Full face. Dorsal surface of head viewed so as to attain the maximum length.

Frontal area. **Character states**: [0] clearly defined; [?] poorly demarcated (by subtle color differences, very feeble or incomplete sutures, or both); or [1] not demarcated.

Frontal sulcus. Sulcus on head extending from frontal area to median ocellus. **Character states**: [0] absent or very feeble (usually visible as a trace of an impressed line, e.g., Figs. 11–14, 33); or [1] conspicuous (e.g., Figs. 27, 38).

HL (*Head length*). Length of head along midline from anterior margin of clypeus to posterior margin of medial portion of the occipital lobe, measured with the head viewed in full face.

HW (*Head width*). Maximum width of head viewed in dorsal full-face, excluding the eyes. Preferred over total length as an index of size. **Character 1, states**: size [0] small (HW 0.90 mm or less); or [1] intermediate to large (greater than 0.90 mm). **Character 2, states:** size [0] small to intermediate (HW less than 1.10 mm); or [1] large (1.10 mm or more).

Labrum shape. **Character states**: in full face view visible (dorsal) part of labrum [0] rounded or truncate (projecting very little; e.g., Figs. 4, 27); or [1] triangular to subtriangular (projecting more conspicuously and coming to a forward point; e.g., Figs. 5, 14).

Occipital lobe. A conspicuous lobe shaped somewhat like an inverted "V" situated immediately above and to the sides of the foramen magnum. The lobe is narrowest above foramen and is most

prominent on either side of head (e.g., Figs. 7–9).

OLI (*Occipital lobe index*). The proportion of the head length measurement accounted for by the median portion of the occipital lobe, multiplied by 100. **Character states**: [0] less than 10; or [1] 10 or more.

Occipital lobe sculpture. **Character states**: (unordered character): lobe [0] smooth; [1] granulate; or [2] rugose.

Orbital grooves. Narrow sulci along the dorsal border of each eye. **Character states**: [0] virtually absent (at most a very narrow, feeble groove; e.g., Figs. 11–14); [?] moderately developed (narrow but readily discernible groove, often with feeble transverse rugae); or [1] conspicuous (groove wider, usually with well-developed transverse rugae; e.g., Figs. 26, 27).

Palpal segmentation. Given in species descriptions as number of segments in maxillary palps; number of segments in labial palps. Because of the limited material counts were made on undissected individuals, when necessary after applying a droplet of relaxing fluid to the mouthparts.

Labial palps. **Character states**: labial palp segments numbering [0] four; [1] three; or [2] two.

Maxillary palps. **Character states**: maxillary palp segments numbering [0] six; [1] five; [2] four; or [3] three.

Postocular distance. The distance between the posterior margin of the eye and the abrupt posterior declivity of the head behind the eye, measured in dorsal full face view (Fig. 38). **Character states**: distance [0] narrow (less than 20% of eye length); or [1] wide (at least 20% of eye length).

Rugae above antennal bases. Narrow rugae curving above antennal fossae, apparently as an extension of the raised borders of the fossae. **Character states**: [0] essentially absent (very short and feeble, or absent); [?] moderately developed (longer, less feeble rugae); [1] conspicuous (rugae well developed, e.g., Figs. 26, 27).

SI (*Scape index*). 100 × SL/HW. **Character states**: [0] 100 or less; [?] intermediate; or [1] 110 or more.

SL (*Scape length*). The maximum length of the scape, excluding the basal radicle.

Trigger hairs. **Character states**: [0] absent, although with two relatively short, slender hairs originating well apart and somewhat ventrad on labrum (Fig. 4), or even more widely separated (in *M. insulcatum*, Fig. 37); or [1] present (two long, thickened hairs originate from adjacent points medially on dorsal surface of labrum; Fig. 5).

Characters on Mandibles

Apical denticles. Relatively very small teeth between the apical and penultimate teeth.

Number. **Character states**: apical denticles numbering [0] two; or [1] one.

Size. **Character states**: longest (most distal) of the apical denticles [0] large (length more than 18% of that of the apical tooth, measuring both from the crotch between them); or [1] small (less than 18%).

Angle, mandibular. Feeble inward bend at a point along outer margin of shafts at about a third the distance from mandible bases to the apical tooth. **Character states**: angle [0] absent (e.g., Fig. 11); or [1] present (Fig. 27).

Apical mandibular bend. In all species the mandible shafts curve gently downwards throughout their lengths when viewed from the side. In addition, however, the shafts are more or less distinctly bent ventrad at about the position of the penultimate tooth. When the bend is strong the apical tooth is conspicuously below the plane of the adjacent teeth. **Character states**: apical bend [0] strong (bend ca. > 35°; Fig. 6A); or [1] feeble (bend or curve of ca. < 20°; Fig. 6B).

Grooves, mandibular. A single, feeble

groove extending longitudinally along the dorsal surface of the shaft of each mandible. **Character states**: [0] absent; [?] very feeble and extending less than half the length of the mandible shafts; [1] present and extending most of the length of mandibular shafts, and positioned either very close to the toothed inner margin of the mandible (character apparently unique to *M. insulcatum*, Figs. 33, 37), or down the middle of the shaft (e.g., Fig. 38).

MI (*Mandible index*). 100 × ML/HL. (For character states see ML [Mandible length].)

ML (*Mandible length*). Measured from the tip of the apical mandibular tooth to the lateral clypeal tooth on the same side as the mandible being measured, with the mandible extending ahead (closed); the measurement was taken with the basal length of the mandible shaft perpendicular to the angle of view. **Character 1, states**: mandible length [0] significantly less than head length (MI < 95); or [1] longer. **Character 2, states**: mandible length [0] longer than head but significantly shorter than trunk (ML/WL < 95); or [1] longer. Queens often have slightly shorter mandibles relative to WL, and so data for queens were not used for character 2 (other than that for the holotype of *M. insulcatum*, which shows state [1]).

Preapical denticles. Denticles (defined as any tooth less than 60% the length of the teeth on either side of it) occurring between teeth proximad to the penultimate tooth. **Character states**: numbering [0] one or more; or [1] entirely absent.

Tooth counts. Counts of the teeth on the mandibles can be useful for species identification, although species do not have a constant number of teeth, as seems to have been assumed previously (indeed, counts for the left and right mandibles of the same specimen often differ by one or two teeth; I therefore generally examined both mandibles).

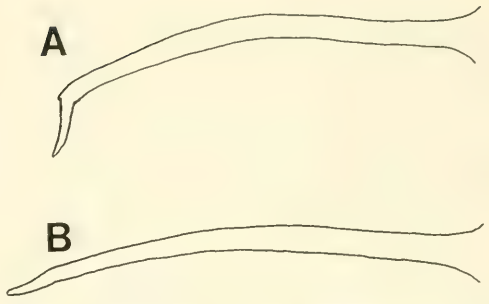


Figure 6. Mandible bend character. Mandibles drawn in lateral view. A. Typical condition in *Myrmoteras*. B. Typical condition in *Myagroteras*.

Mandibular tooth counts exclude preapical and apical denticles (*q.v.*), although since teeth steadily decrease in size basad, the proximal teeth are often smaller than some denticles. **Character states**: mandibles with [0] 8 to 9 teeth; [1] 10 to 13 teeth; or [2] 14 teeth or more (in *M. insulcatum*).

CHARACTERS ON TRUNK, PETIOLE, AND LEGS

HFL (*Hind femur length*). The maximum length of the hind femur. **Character states**: Value for 100 × HFL/HL is [0] 110 or less; [?] intermediate; or [1] 120 or more.

Metanotal groove. When the trunk of a worker is viewed in profile, the position of the metanotal groove is often indicated by a notch. **Character states**: metanotal groove is [0] conspicuously impressed (referring specifically to the presence of a narrow, well-defined notch; Fig. 42); or [1] poorly defined or absent (e.g., Figs. 7, 18).

Metathoracic tubercles. Conspicuous tubercles in workers, on which are located the metathoracic spiracles (Figs. 7, 8).

Metathoracic tubercle pilosity. Prominent hairs rising on or very near the base of each tubercle (workers only). **Character states**: Hairs at each tubercle numbering [0] at least two; or [1] at most one.

Metathoracic tubercle ruga. Ruga clearly

originating immediately anterior to the base of each metathoracic tubercle, which extends forward across mesothorax along dorsolateral margin (found in workers only). **Character states**: Rugae [0] absent; or [1] present (Figs. 7, 8).

Petiolar rugae. With feeble rugae extending transversely across anterior and posterior apices of node summit. **Character states**: rugae [0] absent (summit of node smooth, usually rounded); or [1] present.

Propodeal declivity. **Character states**: declivity of propodeum [0] transversely rugose; or [1] rugae lacking.

Propodeal shape. **Character states**: in workers, dorsum of propodeum [0] flat (e.g., Fig. 45); [?] slightly convex (e.g., Fig. 43); or [1] strongly convex (e.g., Figs. 7, 44).

Sternum of petiole. **Character states**: in profile the portion of the ventral margin of petiole lying directly beneath the node is [0] virtually straight, feebly convex, or feebly concave; or [1] conspicuously convex (e.g., Fig. 34).

TWI (Tibial width index). 100 × the maximum width of the middle tibiae in lateral view divided by their maximum length. **Character states**: middle tibiae [0] relatively thin (TWI < 21); [?] moderately dilated (TWI intermediate); or [1] strongly dilated (TWI > 23).

WL (Trunk length). Distance from the posteriormost point ventrad on the propodeum to the anterodorsal slope of the pronotum, measured with the trunk in profile. Since the pronotum gently curves forward into the cervix, the measurement was taken from the point along the slope where a line tangent to the slope would form an angle of about 45° upon intersecting the plane of the cervix.

LOCALITY DATA AND REFERENCE COLLECTIONS

Locality data for each series conclude with the number of individuals of each caste examined by the author and (in parentheses) the collector(s) of the series, and the museum(s) in which the material is deposited. The latter are designated by the abbreviations that follow: British Museum (Natural History), London (BMNH); Museo Civico di Storia Naturale, Genoa (MCSN); Museum d'Histoire Naturelle, Geneva (MHN); and Museum of Comparative Zoology, Harvard University, Cambridge (MCZ).

Myrmoteras

Myrmoteras Forel, 1893: 607. Type species *Myrmoteras binghami* Forel by monotypy.

Diagnosis. Formicine ants with a distinctive transverse occipital lobe present in all castes. Female castes very similar in appearance, with very large heads; huge, convex eyes; and very long, linear mandibles with well-developed teeth. Males with heads small relative to females; eyes large, convex; scapes long, SI values within range of females; mandibles greatly reduced and without teeth.

Worker. Small to moderately sized (TL 3.9 to 7.0 mm) monomorphic ants belonging to the subfamily Formicinae. Head very large, broader than trunk or gaster, and at least half as long as trunk. Head strongly constricted in back of ocelli so as to form a clearly demarcated occipital lobe which extends transversely across the back of the head; the lobe is narrowed medially above the foramen magnum. Eyes huge, oval and strongly convex, well over half as long as the head length; taking up most of lateral surfaces of head. Ocelli invariably present. A hair originating beneath each compound eye projects forward to either side of clypeus and is usually visible in full face view. Antennae 12-merous; scapes long, gently curved and incrassate distad, invariably extending well beyond occiput; funiculus with segments III generally shortest, terminal segment the longest by far. Antennal fossae positioned dorsally between eyes rather than anterior to eyes as in *Gesomyrmex*; insertions far apart near eye margins and some distance behind the clypeus. Frontal carinae absent, although margins of antennal fossae somewhat raised.

Mandibles slender and extremely elongate, usually longer than head (at minimum 85% as long as head), with the toothed margin running virtually parallel with lateral margins (never subtriangular as in most formicines); somewhat wider than deep in cross section. Mandibular teeth well separated, numbering 8 to 14. The proximal teeth are tiny, but distally the teeth become longer, slender and sharp. There are invariably one or (more commonly) two apical denticles between the apical and penultimate teeth. Mandibles articulated laterally, not relatively close together along anterior margin as in *Odontomachus* (where the front of the head is strongly constricted); nevertheless, the mandibular bases are more approximate than in other formicines because the front of the head is relatively narrow. Clypeus about 25 to 50% wider than long, lacking a feeble medial ridge; generally having a well-developed clypeal tooth at each forward corner and with more or less conspicuous lateral flanges. Clypeus not conspicuously produced, leaving mandible bases and labrum exposed. Labrum elongate, with a small, dorsalmost portion visible in full face view; the remainder projects downward between mandible bases. Palpal formula variable: maxillary 3 to 6; labial 2 to 4 segments.

Trunk (Figs. 7, 8) elongate, widest at pronotum, and somewhat dumbbell-shaped, as the mesothorax is constricted and narrow, with its dorsal and ventral surfaces virtually straight and parallel in profile; pronotum and propodeum relatively massive, convex to flattened above. Metathoracic spiracles raised on conspicuous tubercles. Petiole with prominent peduncles; node broad in front view (usually widest near crown), thick and more or less rounded in profile; never strongly anteroposteriorly compressed. Sternum of petiole virtually without hairs except for a pair of ventrolaterally placed hairs near the base of each peduncle (e.g., Fig. 29). Gaster rounded, with a prominent circlet of hairs around the acidopore; about the size of the head or smaller. Legs long, with tibiae distinctly thicker than femora; middle and hind tibiae often conspicuously dilated.

Queen. Virtually identical to workers in size (including WL and gaster size), proportions and morphology, but alate. Trunk (Fig. 36) high and convex, having a full complement of flight sclerites, and often sculptured somewhat differently than in the worker.

Male. Known only for subgenus *Myrmoteras.* Head small relative to females (Fig. 9), widest immediately behind eyes. Occipital lobe present, well developed. Eyes very large and convex, but relatively smaller than in workers (about half as long as head length); ocelli conspicuous. Antennae 13-merous; relative to head size scape about as long as in females; funiculus long and filiform. Mandibles greatly reduced and edentate, subtriangular with blunt tips; barely extending forward of labrum when opened and not capable of meeting apically at full closure. Forward margin of clypeus rounded, lacking teeth. Palpal segmentation variable as in females.

Trunk (Fig. 10) similar to that of queen. Node of petiole broader than in females; pairs of ventrolateral hairs near bases of peduncles present. Middle and hind tibiae slender relative to females, about as thick as femora. Parameres simple in outline, with narrow, blunt tips and having numerous setae. Pygostyles present. Digitus of volsella heavily sclerotized and strongly curved downwards, coming to a sharp terminal point, and finely serrate along dorsal margin; cuspidal lobes small, rounded. Aedeagus a pair of broad subrectangular plates. (Description of male genitalia based largely on *M. indicum.*)

Fore wings with Mf1 present, and with Rs + M present but somewhat contracted (Brown and Nutting, 1949).

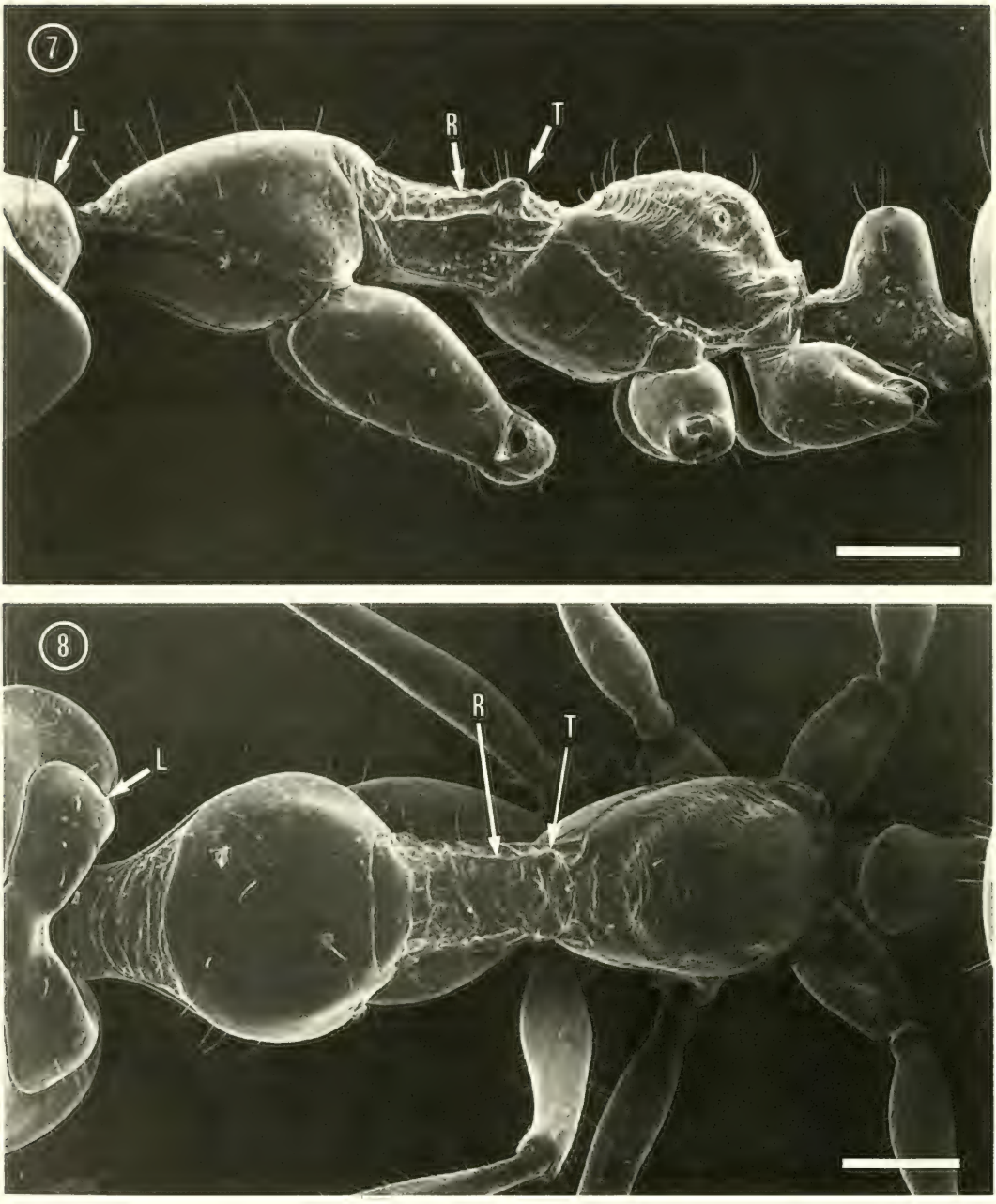
SYNONYMIC LIST OF SPECIES

Subgenus *Myrmoteras* Forel, 1893.

binghami-group.

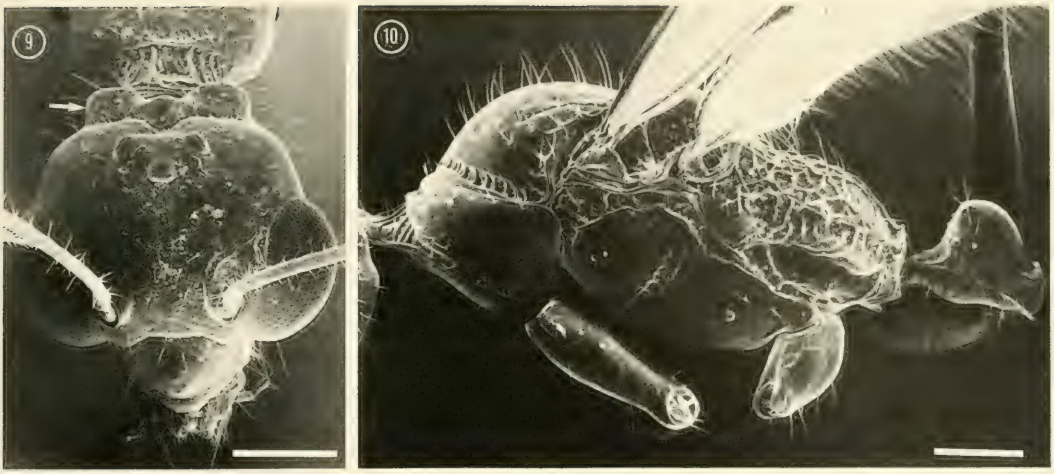
barbouri Creighton, 1930. Java, Peninsular Malaysia, Sabah, Sarawak.

= *kemneri* Wheeler, 1933.



Figures 7–8. Trunk of a *Myrmoteras indicum* worker (series 58 of Besuchet and Löbl). T = metathoracic tubercle; R = metathoracic tubercle ruga; L = occipital lobe. 7. Lateral view. 8. Dorsal view.

Scale lines. 0.25 mm.



Figures 9–10. Male of *Myrmoteras indicum* (series 58 of Besuchet and Löbl). 9. Head (arrow indicates occipital lobe). 10. Trunk.

Scale lines. 0.25 mm.

binghami Forel, 1893. Burma, Thailand.
iriodum sp. nov. Kalimantan, Sarawak, Peninsular Malaysia.
mjoebergi Wheeler (in Creighton, 1930). Borneo (Sarawak?).
ceylonicum-group.
brachygnathum sp. nov. Southern India.
ceylonicum Gregg, 1956. Sri Lanka.
scabrum sp. nov. Southern India.
Subgenus *Myagroteras* new subgenus.
bakeri-group.
bakeri Wheeler, 1919. Sabah, Peninsular Malaysia.
diastematum sp. nov. Sarawak.
indicum sp. nov. Southern India.
donisthorpei-group.
chondrogastrum sp nov. Sarawak.
donisthorpei Wheeler, 1916. Sarawak, Sabah, Kalimantan.
karnyi Gregg, 1954. Mentawai Archipelago.
insulcatum-group.
insulcatum sp. nov. Philippines (Luzon).
williamsi-group.
morowali sp. nov. Sulawesi.
toro sp. nov. Sulawesi.
williamsi Wheeler, 1919. Philippines.
wolasi sp. nov. Sulawesi.

KEY TO *MYRMOTERAS* WORKERS AND QUEENS

The workers and queens of those *Myrmoteras* species in which both castes have been described are very similar except for characters on the trunk. In the key that follows I make the assumption that this holds true for species in which one or the other caste remains undescribed.

1. A pair of long trigger hairs originates from middle of labrum; surface of labrum visible in full face view conspicuously projecting, more or less triangular (Fig. 5); frontal sulcus very feeble or absent (subgenus *Myrmoteras*) 2
– Without trigger hairs; surface of labrum visible in full face view rounded or truncated, not strongly projecting (Fig. 4); frontal sulcus on head usually prominent (subgenus *Myagroteras*) 8
2 (1). Mandibles longer than head (MI > 110); cephalic index < 105; from Southeast Asia (*binghami* group) 3
– Mandibles as long as head or shorter (MI < 105); head wider (cephalic index > 105); from India (*ceylonicum* group) 6
3 (2). In addition to scattered long hairs, pronotum and dorsum of head with numerous very short, fine hairs, and smooth with minute shallow punctures; mandibles lacking denticles except for apical pair ..... *binghami*
– Without short fine pilosity on head and pronotum; sculpture not as described; with one or more denticles on mandible in addition to apical pair 4
4 (3). Head and pronotum distinctly granulate (Fig. 11) ..... *barbouri*
– Head and pronotum smooth or virtually

smooth, with at most traces of granulate sculpture 5

5 (4). Head and trunk shining and smooth except for very poorly defined longitudinal rugae on mesothorax in worker (Fig. 18), and with very sparse long hairs ..... *mjoebergi*

– Head and trunk much less strongly shining, virtually smooth except for mesothorax of workers, which is more lustrous and has conspicuous narrow irregular rugae (Fig. 17); long hairs moderately numerous ..... *triodum*

6 (2). Dorsum of head smooth ..... *brachygnathum*

– Dorsum of head sculptured 7

7 (6). Dorsum of head strongly granulo-rugose (Fig. 21) ..... *scabrum*

– Dorsum of head evenly granulate (Fig. 20) ..... *ceylonicum*

8 (1). Dorsum of head and pronotum granulate or rugose 9

– Dorsum of head and disc of pronotum smooth (except for very feeble rugae on frons of some species) 15

9 (8). Head feebly sculptured; petiole strongly convex beneath node (Fig. 34); with a relatively conspicuous ruga which originates anterior to base of each metathoracic tubercle and extends forward across mesothorax (Fig. 7); maxillary palps with five segments or fewer (*donisthorpei* group) 13

– Head strongly sculptured; petiole feebly convex or concave beneath node; lacking conspicuous narrow ruga described above; maxillary palps with six segments (*williamsi* group) 10

10(9). Evenly granulate all over dorsal and lateral surfaces of head and trunk; in workers mesonotum greatly depressed relative to the pronotum and propodeum, which are very high and rounded (Fig. 44); from the Philippines ..... *williamsi*

– Sculpture different from above; occiput, surface of head beneath eyes, and mesothorax without regular granulate sculpture. In workers pronotum and propodeum not strongly convex, mesonotum depressed, but not strongly so; from Sulawesi 11

11(10). Propodeum of worker moderately convex (Fig. 43); head and pronotum with narrow longitudinal rugae, without granulate sculpture on clypeus ..... *toro*

– Propodeum of worker conspicuously flattened dorsally (Figs. 42, 45); clypeus granulate 12

12(11). Head longitudinally rugose, except for clypeus and frontal area, which are evenly granulate ..... *wolasi*

– Head entirely granulate dorsally, except for frontal area, which is smooth and shining ..... *morowali*

13(9). Gaster granulate dorsally ..... *chondrogastrum*

– Gaster entirely smooth 14

14(13). In worker, propodeum and pronotum high, convex; mesonotum relatively depressed (queen not known) ..... *karnyi*

– Worker with propodeum and pronotum not high and strongly convex, so that summit of propodeum is about level with mesonotum ..... *donisthorpei*

15(8). No trace of frontal sulcus (*insulcatum* group) ..... *insulcatum*

– Frontal sulcus conspicuous (*bakeri* group) 16

16(15). Wide sulcus between clypeus and head capsule (Fig. 26); shallow grooves proceed longitudinally dorsad on mandibles for most of the length of the shafts ..... *diastematum*

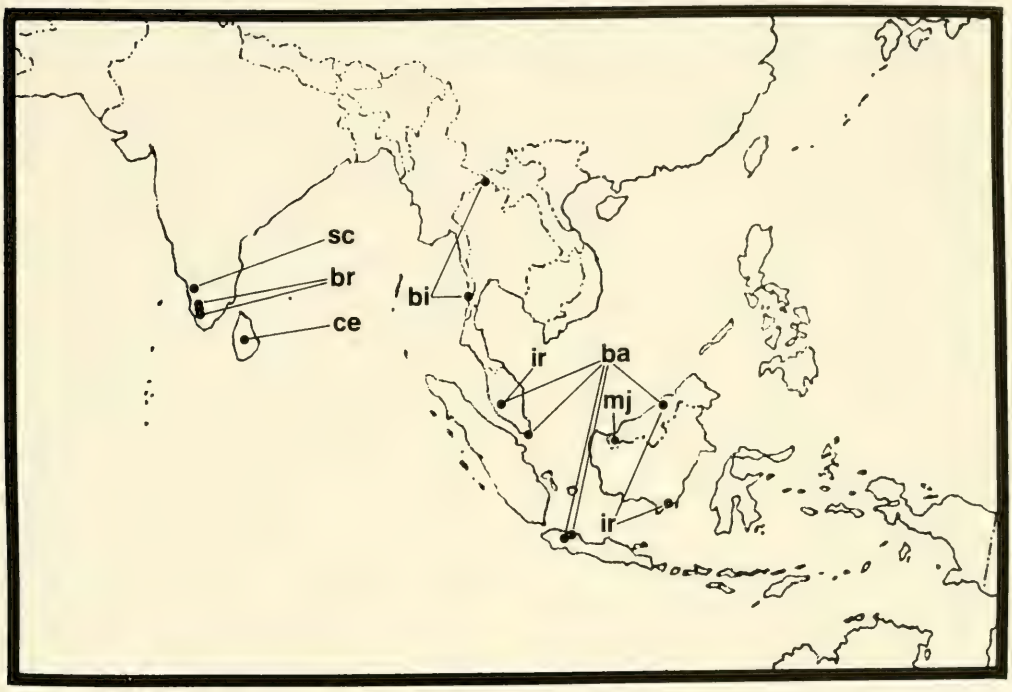
– Very narrow gap between clypeus and head capsule (Fig. 27); grooves on mandibles usually absent or poorly developed 17

17(16). Mandible with two apical denticles, smallest tiny but readily visible; middle tibiae moderately dilated, 16 to 20% as wide as long; propodeum dorsally flattened; from the Malay Archipelago ..... *bakeri*

– Mandible with single apical denticle; middle tibiae thick (26 to 27% as wide as long); propodeum evenly convex; from southern India ..... *indicum*

Subgenus *Myrmoteras*

Workers and queens readily distinguished from subgenus *Myagroteras* by the presence of a pair of prominent trigger hairs. When viewed in perfect full face, the visible part of the labrum is triangular, coming to a more or less distinct forward point from which the trigger hairs originate. Although initially directed somewhat downward and between the bases of the mandibles, the hairs curve gently forward and then extend directly ahead immediately beneath the mandible shafts to 45 to 95% of the distance to the apical tooth. The hairs are much thicker than other body hairs, and are pliable, rarely breaking even in dried material. In some museum specimens the hairs are bent and widely separated. In life, however, the



Map 1. Distribution of species in the subgenus *Myrmoteras*.

Abbreviations: ba = *M. barbouri*, bi = *M. binghami*, br = *M. brachygnathum*, ce = *M. ceylonicum*, ir = *M. iriodum*, mj = *M. mjoebergi*, sc = *M. scabrum*.

hairs are aligned very close together, if not in actual contact through their lengths (Fig. 2).

Frontal sulcus very feeble or absent, usually visible only as a slight trace of an impressed line in some lights; never conspicuous as in *Myagroteras*. Orbital grooves moderately developed to virtually absent; never conspicuous. Narrow ridges curving above antennal carinae absent or moderately developed. Frontal area usually not demarcated at all. Clypeus feebly convex over a broad median region or (in *M. brachygnathum* and *ceylonicum*) more strongly convex; but with lateral flanges somewhat less conspicuous than in *Myagroteras* because shift in plane relative to margins of the raised medial region is reduced.

Mandibles shorter than in most *Myagroteras* species, as long as trunk or shorter (ML/WL < 0.95 except in some *M. iriodum* workers). The mandible shafts bend ventrad about 45° at about the position of the penultimate tooth (less strongly bent in *ceylonicum*). In dorsal view outer margins of shafts proximately virtually straight to feebly convex (becoming progressively more strongly convex distad); without a slight bend at about a third the distance to the mandible tips. Apical denticles often larger and stouter than in *Myagroteras*.

This subgenus contains seven species distributed from India and Sri Lanka to Thailand, peninsular Malaysia, Borneo and Java. Included are all of the largest species of *Myrmoteras* (species with head widths of 1.10 mm or more); however, two species in the *ceylonicum* group are relatively small. The worker is known for all species, the queen for three, and the male for none.

The *binghami* Group

Size medium to large (TL 5.5 to 7.0 mm). Head narrower than in *ceylonicum* group (CI < 102); occipital lobe slightly thicker (OLI 10 to 13). Orbital grooves essentially absent, but the apparent remnants usually visible as extremely narrow, feebly impressed grooves dorsad along margins of eyes. Frontal area not demarcated (except in *M. binghami*, in which the frontal area is visible but ill defined). Ridges above antennal bases essentially absent. Palpal segmentation variable; known extremes 6,4 and 4,3. Mandibles longer than in *ceylonicum* group (MI > 110); number of mandible teeth usually 11 to 13 (8 to 9 in *binghami*). Apical denticles often large, sometimes pair reduced to a single denticle. Mandibles bent ventrad distally to a degree intermediate between that described for *M. ceylonicum* and *M. scabrum* in the *ceylonicum* group; that is, when viewed from above with the basal portion of the shafts perpendicular to the angle of view, the apical tooth and subapical denticles are obviously shifted out of the plane of the other teeth, but not so strongly as to be obscured by the penultimate tooth. Integument lustrous, but in addition head and trunk with a feeble to moderately conspicuous iridescent sheen (virtually lacking on mesothorax) not found in any other species in the genus.

Species in this group are known from Thailand and the Malay Archipelago. What little information is available indicates these ants inhabit moist tropical forests.

Myrmoteras barbouri
Figures 2, 11, 15; Map 1

Myrmoteras barbouri Creighton, 1930: 185, fig. 2; pl. 11, fig. 6. Java, Singdanglalia [Sindanglaja?], 1 worker (T. Barbour, MCZ [examined]).

Myrmoteras kemneri Wheeler, 1933: 73, fig. 1. Indonesia: Java: Tjibodas [=Cibodas], May 29, 1921, 1 worker (N. A. Kemner, MCZ [not found]). PROVISIONAL NEW SYNONYMY.

Diagnosis. *M. barbouri* is readily distinguished from all other species in the *binghami* group by its conspicuous granulate sculpturing.

Worker. Holotype: TL 6.7, HW 1.28, HL 1.25 (CI 102), ML 1.58 (MI 126), SL 1.56 (SI 122), EL 0.76, HFL 1.68 (TWI 21), WL 1.86 mm. Frontal sulcus very feeble, discernible only to height of antennal bases. Palpal segmentation 5,3. Mandibles with 10 teeth and one preapical denticle; apical pair of denticles on both mandibles apparently worn off or broken (not absent as has been supposed by Creighton [1930] and others). Other material of this species has mandibles with 9 to 11 teeth (usually 10) and 1 to 2 preapical denticles (usually 1). The denticle between the penultimate tooth and the one proximad to it is almost half the height of the adjacent teeth and is thus unusually prominent (much less than half the height in other species).

Pronotum slightly flattened above; propodeum evenly convex. Metanotal groove not visible as a conspicuously impressed notch in profile. Node of petiole high and massive, in side view with sloping, straight to slightly concave anterior and posterior faces and with summit narrow relative to base and somewhat flattened (moderately rounded above when viewed from the front). Ventral margin of petiole feebly convex beneath node.

Dorsal surface of head granulate, grain very even and fine (diameters ca. 0.01 to 0.02 mm), similar to *M. ceylonicum* but more delicate; clypeus medially more feebly granulate; back of head virtually smooth. Sculpture on pronotum and propodeum similar to dorsum of head but relatively feeble, particularly on sides; in some lights propodeum appearing to have very feeble transverse rugae across dorsum. Mesothorax with several weak to moderately strong oblique rugae on sides, virtually smooth, but with traces of fine longitudinal rugae dorsally. Pilosity moderately dense, with 20 hairs breaking dorsal margin of trunk in profile. Hairs short, rising 0.08 mm on head and 0.13 mm on trunk and gaster. Two hairs on or near

each metathoracic tubercle, node of petiole with ca. 4 to 8 hairs. Reddish orange, with gaster and antennae yellowish orange, legs same but darker; petiole and mandibles orange.

Queen. Previously undescribed. A single dealate queen from Sabah is tentatively identified with this species. TL 6.9, HW 1.22, HL 1.25 (CI 98), ML 1.69 (MI 136), SL 1.48 (SI 121), EL 0.77, HFL 1.59 (TWI 20), WL 1.93 mm. Granulate sculpture similar but relatively stronger than holotype, as in other material from Borneo (see below). Trunk granulate dorsally, much more feebly granulate on sides; propodeum conspicuously sculptured, transversely granulo-rugose dorsally, obliquely so on sides, with declivity virtually smooth. Uniform rich dark orange red, mandibles, antennae and legs slightly lighter.

Additional Records. BORNEO: *Sarawak:* Fourth Div., Gunung Mulu Nat. Park, RGS Exped., Long Pala, leaf litter, lowland rainforest, 6.X.1977, six workers (B. Bolton, BMNH and MCZ). *Sabah:* Bukit Sulong nr. Lamunin, 4.IX.1982, one dealate queen (N. Stork, BMNH). PENINSULAR MALAYA: Malaysia, Selangor, Ulu Gombak Forest Reserve, 24.VIII.1967, tree lookout area, ca. 450 m, hill forest, one worker (R. Crozier, MCZ); Singapore, Bukit Timah Nat. Reserve, 1 Nov. 1982, in leaf litter on forest floor, one worker (D. H. Murphy and M. W. Moffett, MCZ).

Workers from these regions are similar to the Javanese holotype (including palpal segmentation of 5,3 in all workers examined), but, with the exception of the queen described above, are significantly smaller (HW for workers 1.01 to 1.07 mm; TL 5.8 to 6.1 mm, except Singapore specimen 5.5 mm) and with slightly narrower heads (CI 92 to 96 for all workers); fine rugae on metanotum transverse (continuing partially down sides in Singapore specimen); metanotal groove conspicuously impressed; and with petiole node similar to that described for *M. binghami*: less massive and with a steeper posterior face than in holotype. The Singapore specimen has an exceptionally narrow petiole node. Specimens from Borneo (including the queen described above) are slightly darker in color, have a more strongly developed iridescence and a somewhat stronger granulate sculpturing (but still not as strong as in *M. ceylonicum*); the sculpture continues on occiput (and even feebly beneath head on Sabah queen described above) and on to sides of pronotum and propodeum.

Synonymy. On the basis of Wheeler's (1933) description, the holotype worker of *M. kemneri* is apparently very similar to the *barbouri* type, but is smaller (length given as 6.0 mm, versus 6.9 mm given by Wheeler for the *barbouri* holotype) with a more conspicuous granulate sculpture, slightly darker coloration, and with the petiole having a "distinctly thicker and apically more rounded node" (Wheeler, 1933). These differences are similar to those between the *barbouri* holotype and the Borneo specimens described above.

Natural History. A worker collected in leaf litter at Bukit Timah National Park in Singapore (Fig. 2) could not be induced to capture prey. However, its distinctive movement patterns were so similar to those observed for foragers of *M. toro* from Sulawesi that there can be little doubt *M. barbouri* is also predacious.

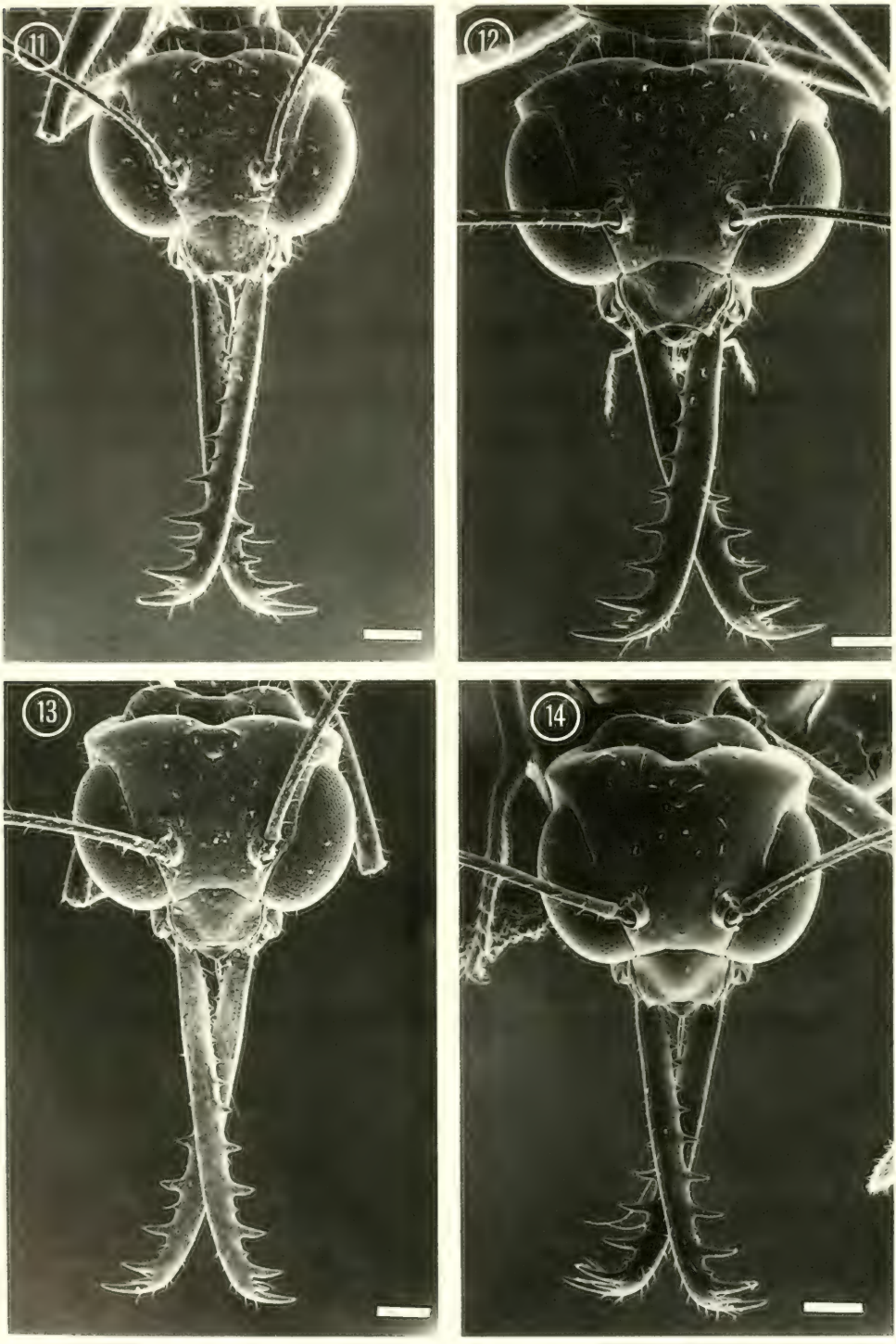
→

Figures 11–14. The *binghami* group. Frontal views of the worker head. 11. *M. barbouri* from Sarawak. 12. *M. binghami* from Thailand. 13. *M. iriodum* paratype. 14. *M. mjoebergi syntype.*

Scale lines. 0.25 mm.

Figures 15–18. The *binghami* group. Lateral views of the worker trunk and gaster. 15. *M. barbouri* from Sarawak. 16. *M. binghami* from Thailand. 17. *M. iriodum* paratype. 18. *M. mjoebergi* syntype (uncoated).

Scale lines. 0.25 mm.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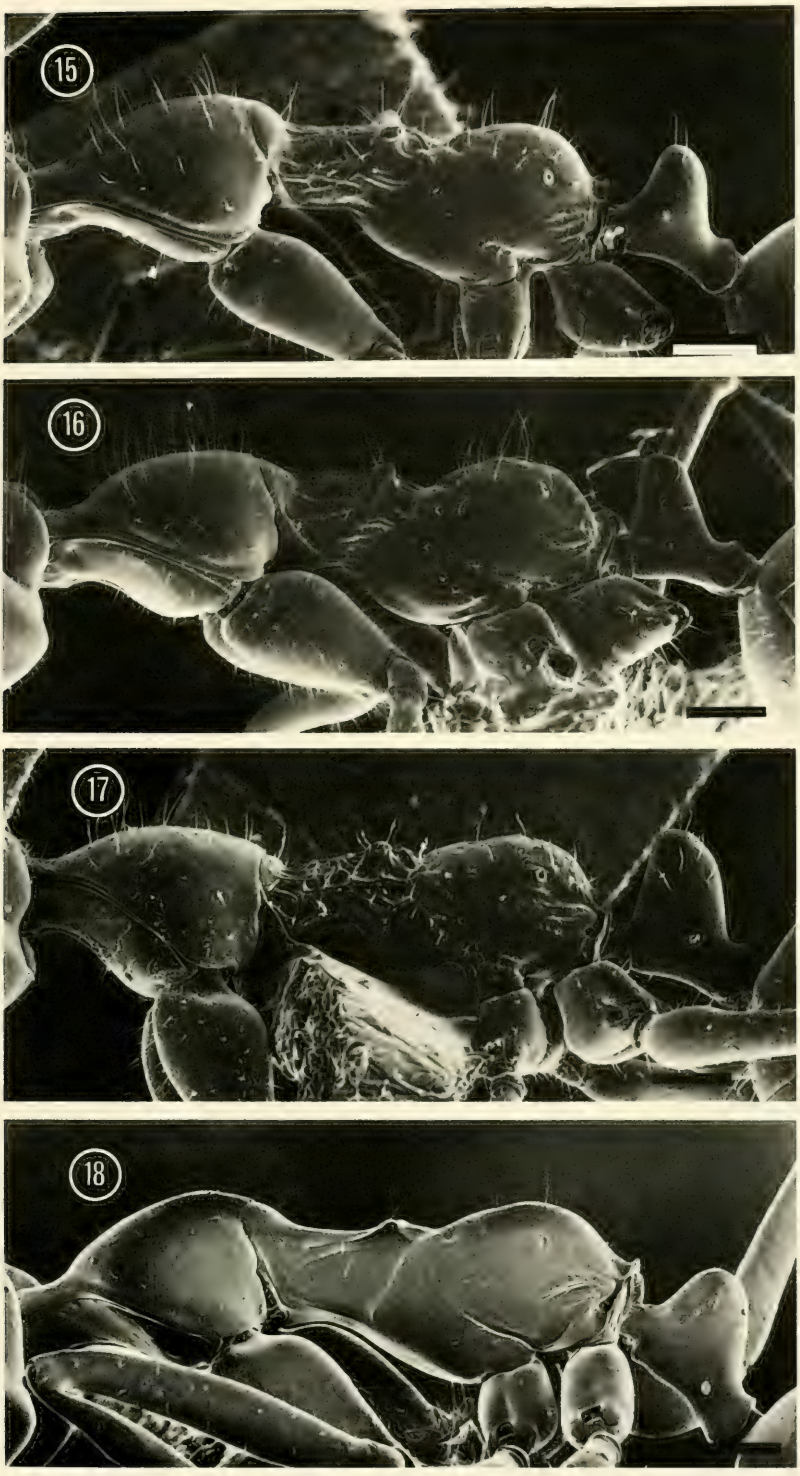
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Myrmoteras binghami
Figures 12, 16; Map 1

Myrmoteras binghami Forel, 1893: 607. Thaungyin Valley (Tenasserim), Burma, May 1893, 2 worker syntypes (Bingham, Forel Coll. [examined]). Worker redescribed by the following: Forel, 1894: 419; Bingham, 1903: 314, fig. 95; Emery, 1925: pl. 1, fig. 10, pl. 2, fig. 1; Creighton, 1930: 186, fig. 2, pl. 11, fig. 2.

Diagnosis. With short decumbent pilosity and minute punctures on the dorsum of the head and pronotum.

Worker. Syntypes (two measured): TL 5.9 mm, HW 1.15 to 1.16, HL 1.15 to 1.17 (CI 99 to 100), ML 1.41 to 1.43 (MI 122), SL 1.38 to 1.40 (SI 120 to 121), EL 0.75, HFL 1.47 to 1.51 (TWI 18 to 20), WL 1.65 to 1.68 mm. Frontal sulcus a very feeble impressed line (Fig. 12)—not conspicuous as has been stated by authors from Creighton (1930) on. Palpal segmentation 6,4 (one worker checked). Frontal area present but poorly demarcated. Mandibles with 8 to 9 teeth and no preapical denticles; two apical denticles.

Pronotum and propodeum slightly flattened above, dorsal face of propodeum shifting to declivity relatively abruptly so as to form a weakly apparent angle (more rounded in other species). Metanotal groove conspicuously impressed. Node of petiole with anterior face precipitous and virtually straight, posterior face not as steep; summit slightly flattened. Ventral margin of petiole feebly concave beneath node.

Pronotum and dorsal surface of head smooth except for numerous minute punctures 0.01 to 0.02 mm apart, including on clypeus; on gaster punctures more widely scattered and weaker; elsewhere with punctures virtually absent. Mesothorax with two to four ill-defined longitudinal rugae low on sides, smooth or with very weak longitudinal wrinkles dorsad; propodeum smooth, although surface very slightly irregular dorsad. In addition to the long, erect to suberect hairs found in other *Myrmoteras* species, with numerous very short, fine decumbent to subdecumbent hairs dorsad on head, pronotum and propodeum and present but less dense and conspicuous on the legs and gaster (one of the syntypes virtually lacks any pilosity dorsad on the head but is otherwise similar to the other; presumably the hairs have been worn off of this area). The long, prominent hairs moderately dense, with 11 to 19 hairs breaking dorsal margin of trunk viewed in profile. Hairs short, rising to 0.08 mm on head and 0.12 mm on trunk and gaster. Two or three hairs on or near each metathoracic tubercle; node of petiole with five to seven hairs. Bright reddish orange, with gaster yellowish brown; petiole, legs, and mandibles orange yellow; and antennae yellowish orange.

Additional Records. BURMA: Thaungyin Valley, one worker (Emery Coll.). THAILAND: Mae Sa [presumably Mae Sai], 19.VII.1975, three workers (D. Jackson, BMNH and MCZ). Burmese specimen similar to syntypes and may be part of the same series. Thailand specimens very similar to syntypes (HW 1.14 to 1.18; TL 5.7 to 5.9 mm; palpal segmentation consistently 6,4) but with relatively shorter mandibles and scapes (MI 128 to 131; SI 112 to 114); much more prominent, smoothly-rounded longitudinal rugae both dorsally and laterally on mesothorax; mesothorax orange, lighter than remainder of trunk; hairs on trunk longer (0.15 mm) and more numerous (29 to 41 breaking dorsal margin in profile); node of petiole with 9 to 11 hairs.

Myrmoteras iriodum new species
Figures 13, 17; Map 1

Holotype. Worker deposited in MCZ from Borneo: SE Kalimantan: 17 to 46 km W. Batulitjin, 28 June to 2 July 1972, lowl. rainfor., hollow stick in litter, B-18, (W. L. Brown). Name a noun in apposition from Gr. *iriodes*, referring to the relatively strong iridescence on the head and trunk.

Diagnosis. Head smooth, lacking sculpture. Distinguished from *M. mjoebergi* by its relatively long mandibles (ML > 1.30), relatively strong iridescence, five-seg-

mented maxillary palps, and by the dense pilosity.

Worker. Holotype (HW 1.20) and five paratypes: TL 6.4 to 6.8, HW 1.14 to 1.20, HL 1.17 to 1.22 (CI 97 to 99), ML 1.68 to 1.74 (MI 142 to 145), SL 1.36 to 1.40 (SI 115 to 120), EL 0.72 to 0.76, HFL 1.49 to 1.56 (TWI 17 to 19), WL 1.80 to 1.85 mm. Only a trace of the frontal sulcus is visible. Trigger hairs unusually short, projecting only ca. 0.45 to 0.50% of distance to mandible tips (ca. 75 to 90% in randomly selected individuals from other species except for two [of four measured] *M. binghami* specimens with measurements of ca. 60%). Palpal segmentation 5,3 (three specimens examined). Mandibles relatively longer than in other species of the subgenus, and with 11 to 13 teeth (usually 12) and 2 to 3 preapical denticles (usually two); apical denticle pair with distal denticle unusually massive, stout. Distal portion of mandible shafts somewhat less strongly bent downward than in *M. mjoebergi.*

Pronotum low and evenly convex; propodeum slightly flattened above. Metanotal groove conspicuously impressed. Node of petiole distinctive, similar to *M. mjoebergi,* but taller and more massive, with anterior face a long vertical drop; summit narrow (relative to base) and rounded; posterior face sloping, slightly convex to straight. Summit of node evenly rounded when viewed from behind. Ventral margin of petiole feebly convex to virtually straight beneath node.

Head and trunk only very feebly lustrous, but more strongly iridescent than in other species, and with other parts of the body more feebly iridescent. Head, pronotum and propodeum smooth (very slight surface irregularities could possibly represent traces of a granulate sculpture); mesothorax very feebly and irregularly rugose dorsad, where rugae are largely transverse. Laterally mesothorax irregularly sculptured with narrow rugae, and in some cases with a narrow ruga extending forward to pronotum from base of metathoracic tubercle, much as in most species of the *donisthorpei* and *bakeri* groups of *Myagroteras.* Pilosity dense to very dense, with 33 to 42 hairs breaking dorsal margin of trunk in profile. Hairs short, rising 0.08 mm on head and 0.10 mm on trunk and gaster. Two or three hairs on or near each metathoracic tubercle; node of petiole with 8 to 14 hairs. Orange with slight reddish tinge, virtually uniform except trunk slightly darker reddish orange and gaster orange yellow.

Queen. Paratype: TL 7.0, HW 1.23, HL 1.24 (CI 101), ML 1.68 (MT 135), SL 1.38 (SI 110), EL 0.77, HFL 1.54 (TWI 18), WL 1.90 mm. Trunk smooth, although possibly with traces of a granulate sculpture; propodeum feebly and irregularly transversely rugose dorsad. Head very feebly longitudinally rugose between bases of antennae.

Paratypes. Six workers with same date and collection number, and one dealate queen with same data but labelled "abandoned earthen termite nest" (MCZ, BMNH).

Additional Records. BORNEO: *Sarawak:* Fourth Div., G. Mulu Nat. Park, RGS Exped., Long Pala, lowl. rainfor. in leaf litter, 13.X.1977, two workers (B. Bolton, BMNH and MCZ). PENINSULAR MALAYA: Selangor, Gombak, 9.X.1973, one worker (B. Bolton, BMNH). All these specimens are similar in size and proportions to the type series (Sarawak workers HW 1.20, 1.28 mm; TL 6.6, 7.0 mm; Gombak worker HW 1.17 mm; TL 6.4 mm), but are somewhat darker (head and trunk orange red to reddish orange, appendages lighter); and with propodeum having very fine, weak, mostly transverse rugae dorsad and behind. Gombak specimen with shape of petiole very similar but with node not as wide and massive as in type series.

Myrmoteras mjoebergi

Figures 5, 14, 18; Map 1

Myrmoteras mjoebergi Wheeler, in Creighton, 1930: 188, fig. 2, pl. 11, fig. 1. Borneo: Mt. Tobangs (top)

(Bukit Tabong? [Sarawak]) 1,700 m, 3 worker paratypes. (E. Mjöberg, MCZ [examined]).

Diagnosis. Head smooth, lacking sculpture. Distinguished from *M. iriodum* by its shorter mandibles (MI < 130), four-segmented maxillary palps, low, rounded petiolar node, and greatly reduced pilosity.

Worker. Syntypes (three measured): TL 5.6 to 6.0, HW 1.02 to 1.08, HL 1.12 to 1.18 (CI 91 to 92), ML 1.26 to 1.31 (MI 111 to 112), SL 1.21 to 1.27 (SI 116 to 119), EL 0.66 to 0.71, HFL 1.43 to 1.55 (TWI 17 to 18), WL 1.60 to 1.70 mm. Frontal sulcus absent (slightest trace between antennae in some lights). Palpal segmentation consistently 4,3. Mandibles with 10 to 12 teeth (usually 10) and one to two preapical denticles (usually two); apical pair with larger (most distal) denticle thinner and generally coming to a sharper point than in other species in the *binghami* group.

Pronotum higher and more rounded than in other species in the subgenus; propodeum also convex, slightly flattened dorsad in one specimen. Metanotal groove not visible as a conspicuously impressed notch in profile. Propodeum evenly and feebly convex in profile. Node of petiole low, rounded; anterior face more precipitous. Ventral margin of petiole feebly convex or feebly concave beneath node.

Head and trunk smooth, lacking punctures or other traces of sculpture outside of poorly defined longitudinal rugae on sides of mesothorax. Hairs short and sparse, rising about 0.10 mm, with 8 to 12 rising above dorsal margin of trunk in profile. Metathoracic tubercle hairs one or none; node of petiole with ca. five to seven hairs. Head and trunk uniform orange red, petiole orange, gaster yellow brown; legs, antennae, and mandibles strongly contrasting orange yellow.

Additional Records. Known only from type series.

The *ceylonicum* Group

Small to medium species (worker 3.9 to 5.5 mm TL). Head broad (CI > 108); occipital lobe slightly less massive than in *binghami* group (OLI 5 to 8). Orbital grooves moderately developed, more conspicuous than in the *binghami* species group. Frontal area present but poorly demarcated (absent in *brachygnathum*). Ridges above antennal bases moderately developed. Palpal segmentation variable; known extremes 6,4 and 3,3 (4,2 in *M. scabrum*?). Mandibles conspicuously shorter than in any other species, no longer than head (MI less than 102). Number of mandibular teeth eight to nine; apical denticles both present, but small. Head and trunk lustrous, completely lacking the feeble iridescent sheen typical of the *binghami* group.

This distinctive group includes three species from southern India and Sri Lanka, all of which have been collected in areas of evergreen forest at moderate to high elevations (600 to 2,200 m).

Myrmoteras brachygnathum new species
Figures 19, 22; Map 1

Holotype. Worker deposited in MHN from India: Tamil Nadu: Palni Hills, south of Kodaikanal, 2,200 m, 12.XI.72, #23 [tamisages dans forêt dégradée avec rhododendrons] (Besuchet and Löbl). Name derived from Gr. *brachys* + *gnathum*, referring to the relatively short mandibles of the females.

Diagnosis. Easily distinguished from *M. ceylonicum* and *scabrum* by the lack of sculpture on the head and pronotum.

Worker. Holotype: TL 3.9, HW 0.92, HL 0.85 (CI 109), ML 0.73 (MI 86), SL 0.90 (SI 97), EL 0.56, HFL 0.94 (TWI 20), WL 1.18 mm; paratype worker from same series TL 4.0, HW 0.93 mm, and otherwise virtually identical to holotype. Only a trace of the frontal sulcus is visible. Frontal area not demarcated. Clypeus highly convex, with curvature continuing to lateral margins, as in *M. ceylonicum* but unlike any other species in the subgenus. In *M. brachygnathum* the clypeus also exceptionally narrow, only 23 to 25% wider than long (greater than 35% for single specimens selected at random from all other species in the genus, including *cey-*

lonicum). Palpal segmentation of type 3,3 (in paratype worker 4,3). Mandibles with one to two preapical denticles. Curvature of distal ends of mandible shafts ventrad stronger than described for *M. ceylonicum* but still relatively weak; bend at penultimate tooth about 30 to 40°.

Pronotum low and evenly convex or slightly flattened; propodeum rounded, summit somewhat higher than mesothorax (virtually level with mesothorax in other species in the subgenus). Metanotal groove conspicuously impressed. Node of petiole tall, with nearly vertical posterior face and very steep, straight anterior face; summit slightly flattened, but lacking the transverse ridges found in *M. ceylonicum* and *scabrum*. Spurs on middle and hind tibiae shorter than in other members of the subgenus, longest with a length of about twice the width of the base of the first tarsal segment.

Head, pronotum and propodeum smooth and polished, lacking sculpture. Mesothorax with two to three narrow longitudinal rugae on sides, weaker longitudinal rugae dorsally. Pilosity considerably reduced in comparison to *M. ceylonicum* and *scabrum*, with hairs sparse, 2 to 10 breaking dorsal margin of trunk in profile. Hairs rising 0.08 to 0.10 mm on head, trunk, and gaster. One or no hairs on or near each metathoracic tubercle; node of petiole with two to four hairs. Head and trunk translucent yellowish orange (rugae on mesothorax darker), antennae same but lighter; petiole orange yellow, legs and mandibles lighter orange yellow; gaster very dark orange brown.

Queen. Dealates from type series (one measured; other virtually identical), TL 4.3, HW 1.03, HL 0.92 (CI 112), ML 0.81 (MI 88), SL 0.98 (SI 95), EL 0.63, HFL 1.03 (TWI 20), WL 1.33 mm; very similar in shape and proportions to worker except for more massive trunk; petiole similar but narrower at summit. Trunk entirely smooth and shining, reddish orange; otherwise color same as in workers.

Paratypes. One worker and two dealate queens with same locality data and collection number as holotype (MCZ and MHN).

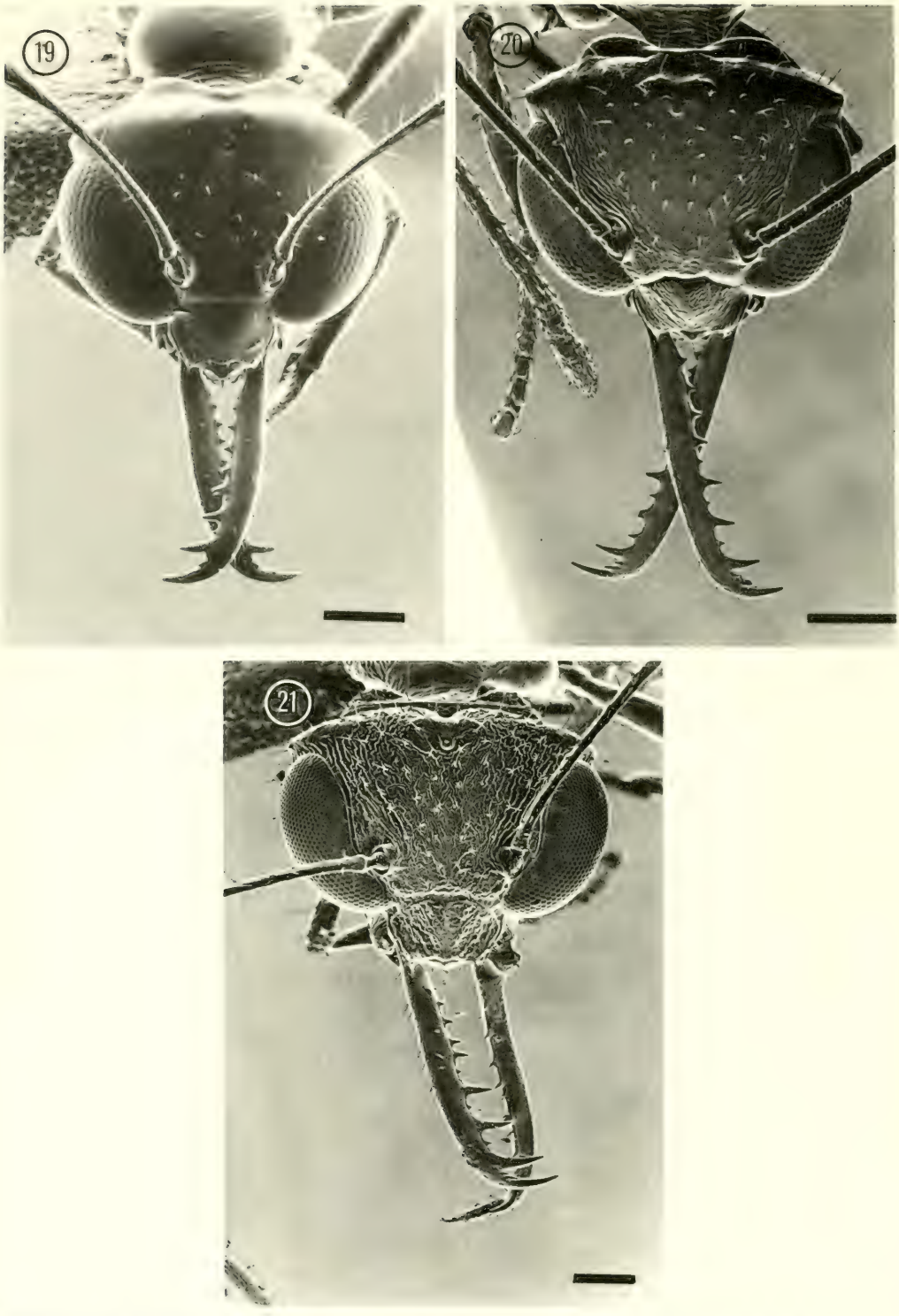
Additional Records. INDIA: *Tamil Nadu:* Kodaikanal, 17.4.27, one dealate queen (C. Escher, MHN); Palni Hills, 7 km east of Kodaikanal, 1,750 m, 12.XI.1972, #24 [tamisages en forêt], 23 workers (Besuchet and Löbl, MHN, MCZ, MCSN); Palni Hills, 10 km east of Kodaikanal, 2,150 m, 15.XI.1972, #27 [tamisages en lisière de forêt, avec rhododendrons et fougères, près d'une rivière], one worker, three dealate queens (Besuchet and Löbl, MHN); Anaimalai Hills, 18 km north of Valparai, 1,250 m, 18.XI.1972, #35 [tamisages en forêt], four workers, one dealate queen (Besuchet, Löbl, and Mussard, MHN, BMNH, MCZ). Palpal segmentation 4,3 in all females checked (at least four in each series, when available); pilosity consistently sparse, with no more than 15 hairs breaking dorsal margin of trunk in profile.

Myrmoteras ceylonicum
Figures 20, 23; Map 1

Myrmoteras ceylonica Gregg, 1956: 41, fig. 1. Sri Lanka: Udawaddatekele Sanctuary, Kandy, 2,000 ft, VII.13.1955, #1243, three workers (E. O. Wilson, holotype in MCZ [examined]; paratypes in collection of R. E. Gregg). Name changed to correspond in gender with genus.

Diagnosis. Head and trunk conspicuously sculptured. Distinguished from *M. scabrum* by its smaller size; evenly granulate head sculpture; relatively feeble mandibular bend; dorsally flattened pronotum; node of petiole taller than wide in side view; and lighter color.

Worker. Holotype: Length excluding missing gaster 3.1 mm (est. original TL 4.0 mm), HW 0.94, HL 0.83 mm (not 0.90 mm, as Gregg [1956] reported) (CI 113), ML 0.83 (MI 100), SL 0.85 (SI 90), EL 0.56, HFL 0.95 (TWI 28), WL 1.17 mm. Size small. Frontal sulcus very feeble, a narrow smooth line extending from just above clypeus to median ocellus. Frontal area poorly defined. Clypeus strongly convex, as described for *M. brachygnathum*



Figures 19–21. The *ceylonicum* group. Frontal views of the worker head. 19. *M. brachygnathum* paratype. 20. *M. ceylonicum* holotype (uncoated; oil slightly obscures sculpture). 21. *M. scabrum* holotype (uncoated).

Scale lines. 0.25 mm.

Figures 22–24. The *ceylonicum* group. Lateral views of the worker trunk and gaster. 22. *M. brachygnathum* paratype. 23. *M. ceylonicum* holotype (uncoated; oil slightly obscures sculpture). 24. *M. scabrum* holotype (uncoated).

Scale lines. 0.25 mm.

but not as narrow. Scapes relatively short, overreaching posterior border at 62% of their length. Palpal segmentation 6,4. Mandibles with 3 to 4 preapical denticles. Mandible shafts weakly bent downward distally, so that when seen from above with the proximal portions of the shafts in the plane of view both the apical tooth and apical denticles are clearly visible; bend at penultimate tooth only about 35°.

Pronotum and propodeum flattened dorsad. Metanotal groove conspicuously impressed. Petiole with node narrow, much taller than broad in side view, with steep, virtually straight sides and a flat or slightly concave summit with feeble ridges along the apices of the anterior and posterior faces; short and squat when viewed from behind. In holotype curvature of ventral margin of petiole beneath node uncertain because of obscuring glue (illustration of Gregg [1956], which is of doubtful value because it is based on the same specimen, shows ventral margin virtually straight except for a small scooped-out area near the anterior peduncle). Tibia of the single intact middle leg on the holotype strongly dilated (in other species in the subgenus TWI 16 to 22).

Dorsal surface of head evenly granulate, with grains ca. 0.01 to 0.02 mm in diameter; clypeus finely granulo-rugose; back of head smooth. Smooth laterally beneath eyes except for faint longitudinal rugae; ventrum of head smooth. Pronotum more weakly granulate than head, smoother laterally; mesothorax with 2 to 3 widely spaced longitudinal rugae on sides and more numerous and weaker longitudinal rugae above; propodeum almost smooth laterally, dorsally and behind with narrow, relatively straight and evenly spaced transverse rugae ca. 0.03 mm apart. Pilosity long and dense, with 37 hairs breaking dorsal margin of trunk viewed in profile. Hairs rising 0.13 mm on head and 0.20 mm on trunk. Two prominent hairs on or near each metathoracic tubercle; six hairs on node of petiole. Reddish orange but with petiole, legs, gaster and antennae orange yellow and mandibles lighter orange yellow.

Additional Records. Known only from type series.

Myrmoteras scabrum new species
Figures 21, 24; Map 1

Holotype. Worker deposited in MCZ from India: Kerala State: Cannanore Dist.: Peria Reserve (Western Ghats), 4–5.IV.1969, ca. 900 m, evgrn. for. (A. B. Soans and W. L. Brown). Name derived from Latin *scabra*, referring to the heavily sculptured head and trunk.

Diagnosis. Head and trunk conspicuously sculptured. *M. scabrum* can be distinguished from closely related *ceylonicum* by its larger size; the stronger granulo-rugose sculpture on the head; very conspicuous mandible bend; evenly convex (rather than flattened) pronotum; node of petiole wider than tall in side view; and much darker color.

Worker. Holotype: TL 5.5, HW 1.25, HL 1.12 (CI 112), ML 1.13 (MI 101), SL 1.31 (SI 105), EL 0.73, HFL 1.38 (TWI 16), WL 1.68 mm. Larger than *M. ceylonicum* and *brachygnathum*. Frontal sulcus absent, although a weak medial ridge extends from clypeus to a point just above antennal bases. Frontal area present, better defined than in *M. ceylonicum*. Scapes relatively longer than in *M. ceylonicum* holotype, overreaching posterior border of head at about 50% of their length. Clypeus raised medially somewhat more prominently than in most species in the subgenus but not to the degree found in *M. ceylonicum* and *brachygnathum*; clypeal teeth exceptionally strong. Maxillary palps four, labial palps apparently two. Mandibles with two to three preapical denticles; shafts strongly bent at tips, so that when seen from above with the proximal portions of the shafts in the plane of view the apical tooth and apical denticles are virtually directly behind the penultimate tooth. Mandibles relatively strongly depressed, 46% wider than deep

at position of fifth tooth (about half way to apex); in single specimens selected at random from each of the other species in the subgenus the mandibles varied from 26 to 35% wider than deep at this point.

Trunk as described for *M. ceylonicum* but propodeum less strongly depressed. Anterior and (except at base) posterior faces of petiolar node virtually straight, with the anterior face steeper, meeting peduncle rather abruptly at an obtuse angle; posterior face curving gently into posterior peduncle. Summit of node flat or slightly concave in profile as in *M. ceylonicum*, with ridges along anterior and posterior apices somewhat better developed. Node 20% broader than high, versus 45% higher than broad in *ceylonicum*. Middle and hind tibiae only slightly swollen, parallel sided throughout most of their lengths.

Dorsal surface of head densely granulorugose, coarser (grain ca. 0.02 to 0.03 mm across) and more irregular than in *M. ceylonicum*; this sculpturing weaker and less dense on clypeus (which is virtually smooth mesad) and on back of head. Smooth laterally beneath eyes except for faint longitudinal rugae; ventrum of head smooth. Pronotum densely and very irregularly rugose, rugae largely transverse; mesothorax with prominent longitudinal rugae ca. 0.04 mm apart dorsad and laterally; similar rugae laterally on propodeum. Propodeum dorsally and behind with narrow transverse rugae as in *M. ceylonicum* but more closely spaced, ca. 0.02 to 0.03 mm apart. Gaster and legs smooth and shining. Pilosity very dense, with more than 40 hairs breaking dorsal margin of trunk in profile. Hairs long, rising to 0.15 mm on head and 0.20 mm on trunk and gaster. Two hairs on or near each metathoracic tubercle; node of petiole with two rows of five to six well-spaced hairs along anterior and posterior ridges and down onto sides of node. Very dark orange red with legs and gaster relatively lighter and antennae and mandibles yellowish orange; tarsi yellow.

Additional Records. Known only from holotype.

Subgenus *Myagroteras* new subgenus

Type. Myrmoteras donisthorpei Wheeler, by present selection. Name derived from Gr. *myagra* + *teras*, in reference to the trap-jaw prey capture technique.

Females lacking the long trigger hairs characteristic of the subgenus *Myrmoteras*; instead labrum with a pair of short but conspicuous hairs (length less than 10% of mandible length). Dorsal surface of labrum (that is, the surface visible in dorsal full face view) not coming to a distinct anterior point; instead anterior margin rounded or truncate. The paired hairs originate well apart somewhat below the dorsal labral surface, and thus they are apparently positioned relatively lower on labrum than are trigger hairs in the subgenus *Myrmoteras*. The hairs are straight, and extend forward and strongly ventrad. Although more slender and differing somewhat in position, these hairs are possibly homologous with the trigger hairs found in the subgenus *Myrmoteras*.

In contrast to the subgenus *Myrmoteras*, frontal sulcus strongly developed, a conspicuous narrow to moderately wide groove (maximum width at least 0.01 mm) extending from the frontal area to the median ocellus (the single exception is *M. insulcatum*, which completely lacks the sulcus). Both the orbital grooves and the ridges above antennal bases present, moderately developed to conspicuous. Frontal area demarcated to some degree. Except for the species *M. insulcatum*, clypeus higher and more strongly convex medially than in the subgenus *Myrmoteras*, and with lateral flanges better defined because of a more sudden shift in plane relative to the margins of the median region.

Mandibles relatively longer than in *Myrmoteras*, usually as long as or longer than trunk (ML/WL > 0.95 except in some *M. morowali* and *indicum* workers). Mandible shafts very feebly bent ventrad

at position of penultimate tooth, angle of bend 20° or less (Fig. 6B); bend strongest in *M. williamsi*. When viewed from above outer margins of shafts feebly convex as in *Myrmoteras*, but often with a subtle inward bend at about a third of the distance from the mandible bases to the apical tooth (Fig. 27; essentially lacking in *M. toro, diastematum*, and some *donisthorpei* workers). Apical denticles relatively poorly developed, often smaller than in the subgenus *Myrmoteras*, with the largest invariably less than 18% of the length of the apical tooth.

Myagroteras species tend to be small, with none having head widths exceeding 1.10 mm. None of these ants has the feeble iridescence on the head and trunk characteristic of the *Myrmoteras* species in the *binghami* group.

This subgenus contains 11 species distributed from India to the Philippines. To date the greatest number of *Myagroteras* collections have been made in Borneo. The worker caste is known for ten species; the queen for nine; and males for four.

Two males have been collected from Hainan Island; one from Tien Fong Mountains is in the British Museum (Natural History) and the other (from Ta Han) is in the Museum of Comparative Zoology. Both are very similar to males of *M. bakeri* and *donisthorpei* and are therefore presumably in the subgenus *Myagroteras* (no males from the subgenus *Myrmoteras* have been described).

The *bakeri* Group

Mostly medium-sized (female size range 4.2 to 6.0 mm); smallest species *M. bakeri*. Palpal segmentation varying from 5,3 to 4,2. Head and pronotum smooth, lacking sculpture, or with only traces of rugae. Rugae above antennal bases often conspicuous. Mandibles often with only a single apical denticle. Narrow ruga extends forward from base of each metathoracic tubercle as in the *donisthorpei* group (but absent in *M. bakeri*). Metanotal groove not visible as a conspicuously impressed notch in profile (but notch feebly developed in some *M. bakeri*). Ventral margin of petiole feebly convex beneath node.

Two species in this group are from Malaysia (including Sarawak and Sabah) and the third is from southern India.

Myrmoteras bakeri
Figures 25, 28; Map 2

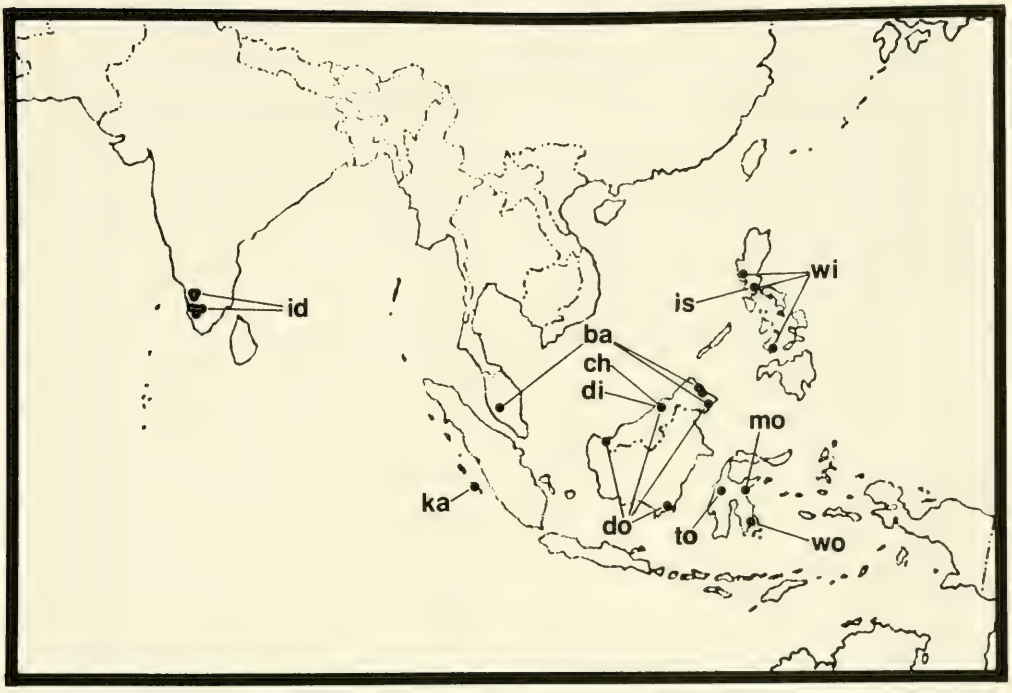
Myrmoteras bakeri Wheeler, 1919: 145. Borneo: Sabah: Sandakan, 1 queen and 3 males (Baker, MCZ [examined]). Creighton, 1930: 184, pl. 11, fig. 5.

Diagnosis. Females can be distinguished from other species in the *bakeri* group by the absence of a wide sulcus between the clypeus and frons; the lack of a prominent ruga extending forward from each metathoracic tubercle; the presence of two apical denticles on each mandible; and the relatively dilated tibiae (TWI > 23).

Workers. Described for the first time. The following description applies to two workers from Sabah collected by Leakey. TL 4.6, HW 0.86 to 0.89, HL 0.88 (CI 98 to 102), ML 1.33 to 1.34 (MI 152 to 153), SL 0.94 to 0.95 (SI 107 to 109), EL 0.56 to 0.58, HFL 0.94 to 0.96 (TWI 26 to 27), WL 1.23 to 1.25 mm. Frontal sulcus a narrow, very shallow trench; orbital grooves conspicuous. Frontal area clearly defined. Palpal segmentation 5,3 (both inspected). Mandibles with 11 to 12 teeth and two preapical denticles. With two very tiny and sharp apical denticles, the smallest minute.

Pronotum low and evenly convex; propodeum feebly convex, and with summit virtually level with mesothorax; metanotal groove visible as a feebly impressed notch in profile. Node of petiole in profile with nearly vertical anterior face. Tibiae strongly dilated as in *M. donisthorpei*, but unlike other members of the *bakeri* and *williamsi* groups, which have feebly dilated tibiae.

Head smooth except for traces of very fine longitudinal rugae between antennal

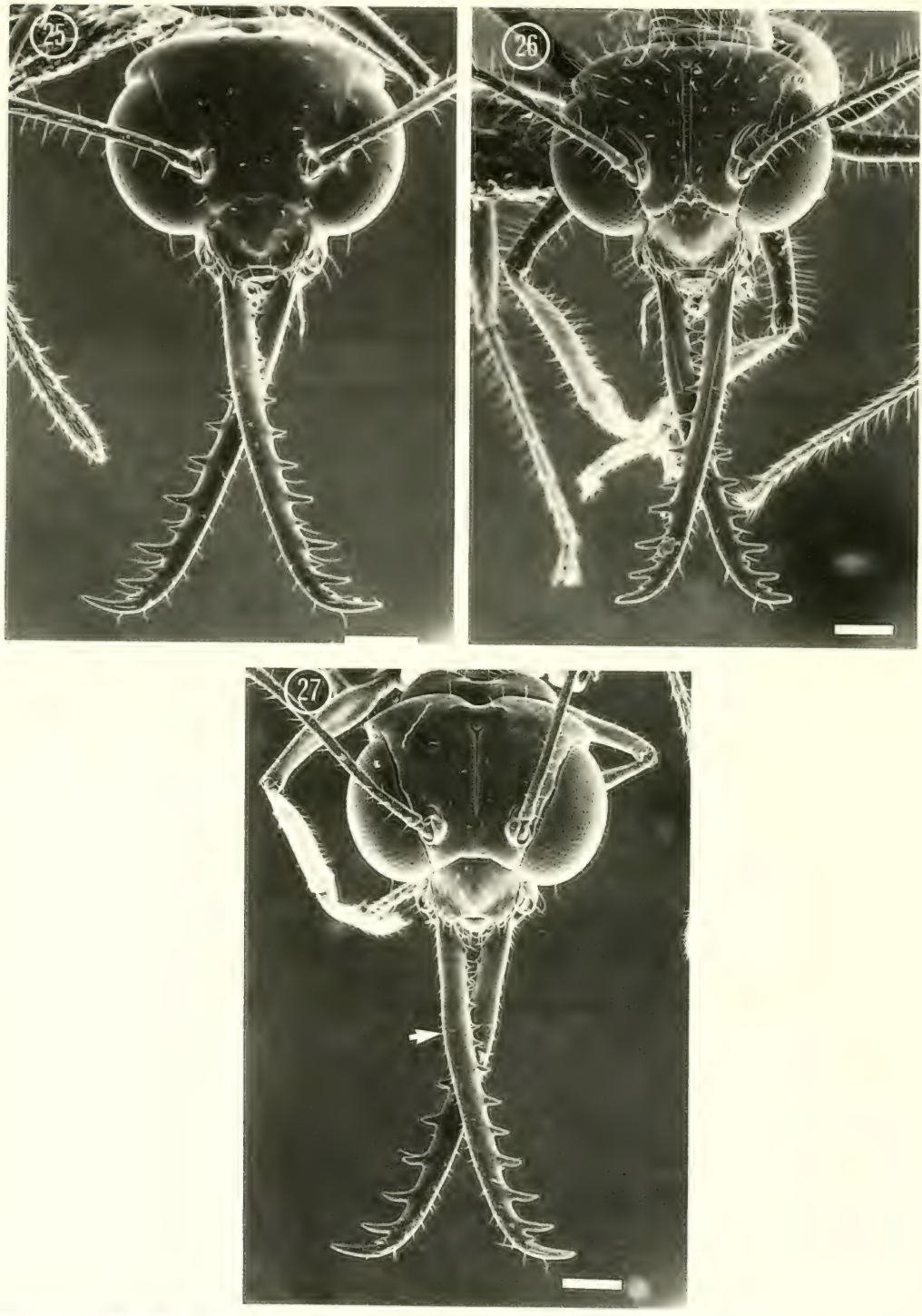


Map 2. Distribution of species in the subgenus *Myagroteras*.

Abbreviations: ba = *M. bakeri*, ch = *M. chondrogastrum*, di = *M. diastematum*, do = *M. donisthorpei*, id = *M. indicum*, is = *M. insulcatum*, ka = *M. karnyi*, mo = *M. morowali*, to = *M. toro*, wi = *M. williamsi*, wo = *M. wolasi*.

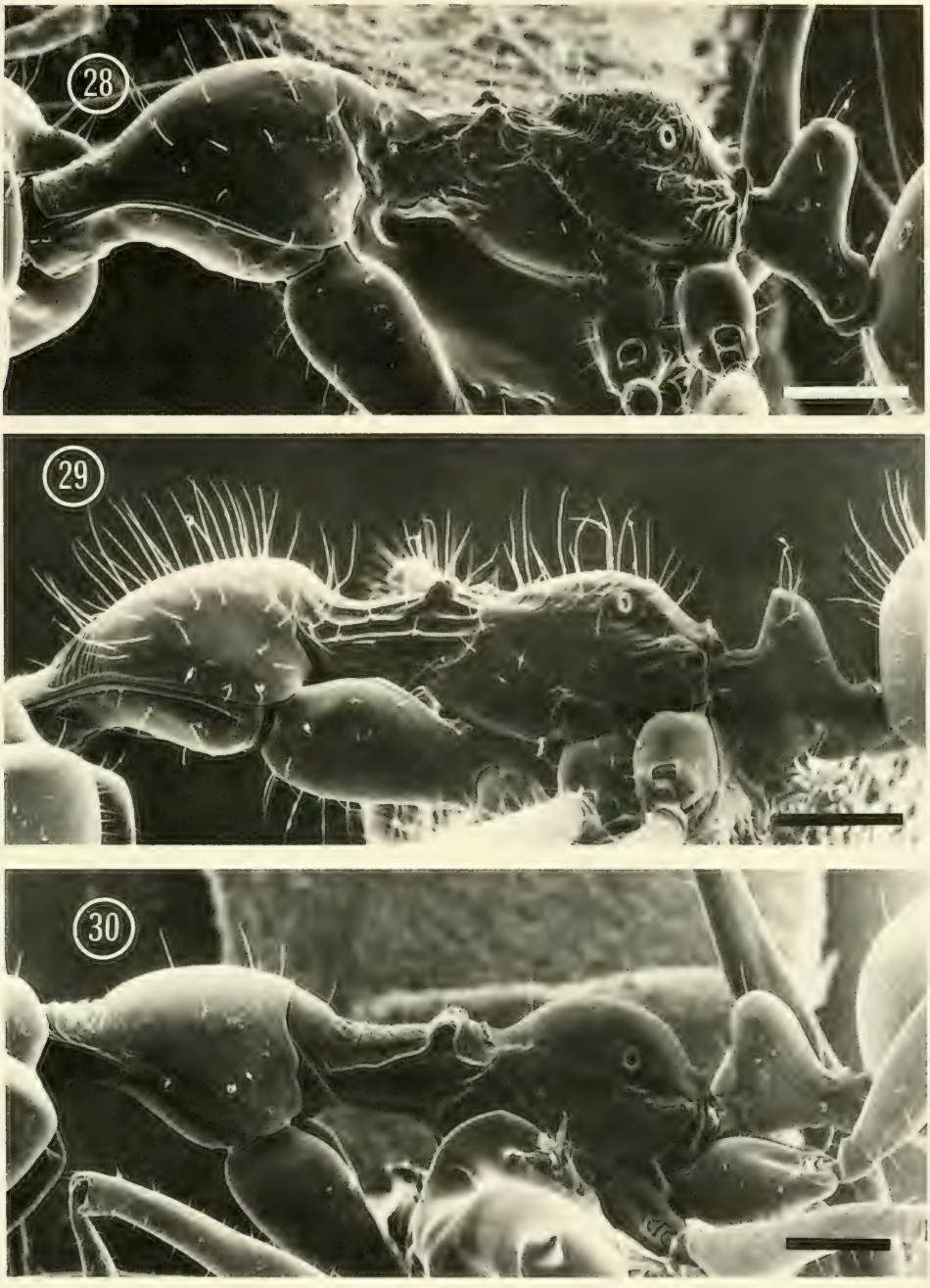
bases and rugae curving above antennal fossae. Pronotum smooth but with traces of longitudinal rugae dorsally; dorsum of mesothorax feebly granulate with delicate transverse rugae, laterally smooth except for feeble oblique or longitudinal rugae; propodeum with very fine transverse rugae dorsally, extending obliquely over sides, posterior declivity smooth. Pilosity moderately dense, with 19 to 21 hairs breaking dorsal margin of trunk in profile. Hairs short, rising 0.06 mm on head and 0.10 mm on trunk and gaster; two to three hairs on or near each metathoracic tubercle; five to six on node of petiole. Uniform yellowish orange with appendages and petiole lighter, orange yellow (femora and coxae virtually white); gaster darker. Head translucent as in queen.

Queen. Holotype with head, petiole and gaster lost: HFL 0.87 (TWI 24), WL 1.18 mm. A second queen from the same region, apparently very similar to holotype: TL 4.2, HW 0.82, HL 0.83 (CI 100), ML 1.23 (MI 148), SL 0.88 (SI 106), EL 0.54, HFL 0.85 (TWI 26), WL 1.15 mm. Creighton (1930) states that the mandibles of the holotype had nine teeth and two preapical denticles, as well as only a single apical denticle; the other queen has 10 to 11 teeth and two preapical denticles, as well as a pair of tiny apical denticles, as in the workers. Trunk smooth except for very feebly rugulose sculpture on mesonotum near scutellum; propodeum transversely rugose dorsad, these rugae extending obliquely onto sides; rugae ca. 0.01 mm across. Trunk of holotype yellowish orange, lighter than in workers, with petiole and legs pale yellow, femora, trochanters and coxae virtually white; the other queen is similarly colored, with the



Figures 25–27. The *bakeri* group. Frontal views of the worker head. 25. *M. bakeri* from Sabah (fine layer of oil obscures frontal sulcus). 26. *M. diastematum*. 27. *M. indicum* paratype (arrow indicates location of mandibular angle).

Scale lines. 0.25 mm.



Figures 28–30. The *bakeri* group. Lateral views of the worker trunk and gaster. 28. *M. bakeri* from Sabah. 29. *M. diastematum*. 30. *M. indicum* paratype.

Scale lines. 0.25 mm.

head concolorous with trunk and translucent, as had been described for the holotype (Creighton, 1930). This translucence is of doubtful taxonomic value, because the head is opaque in a Malayan *M. bakeri* specimen. Some specimens of *M. diastematum* and *M. indicum* also have relatively translucent integuments.

Male. Paratypes (two measured): HW 0.63, HL 0.68 (CI 93), SL 0.78 to 0.83 (SI 124 to 132), EL 0.35 to 0.37, WL 1.04 to 1.09 mm. Frontal sulcus a feebly impressed medial line. Palpal segmentation 5,3. Head smooth; mesonotum and scutellum longitudinally rugulose, rugae ca. 0.01 to 0.02 mm across; pronotum and anepisternum much more feebly rugulose; katepisternum and propodeum with conspicuous raised rugae; these extend mostly longitudinally on sides and transversely dorsad and on posterior declivity. Sculpture on trunk interspersed with a little granulate sculpture.

Additional Records. BORNEO: *Sabah:* Gunung Silam, 620 m, 1983, A15-3.1, two workers (R. Leakey, BMNH and MCZ); Bettotan near Sandakan, 12 Aug. 1927, one alate queen (C. B. K. and H. M. P., BMNH). PENINSULAR MALAYA: Selangor, Gombak, 9.X.1973, one worker (B. Bolton, BMNH). Worker from the Malay Peninsula slightly smaller in size than the Sabah workers (TL 4.2, HW 0.83), but very similar in proportions; rugae between antennal bases more prominent but still feeble; propodeum much more feebly rugulose, with dorsum essentially smooth; metanotal groove poorly defined; with a feeble groove running most of the length of each mandible dorsally, as in *M. diastematum* and *morowali* females.

Myrmoteras diastematum new species
Figures 26, 29; Map 2

Holotype. Worker deposited in BMNH from Borneo: Sarawak: 4th Division: Gunung Mulu National Park, v–viii.1978, B. M. 1978-49, camp 2 (P. M. Hammond and J. E. Marshall). Name derived from Gr. *diastema*, referring to the wide sulci on the head.

Diagnosis. The conspicuous sulcus between the clypeus and frons is unique to this species; this and the exceptionally wide frontal sulcus and orbital grooves serve to readily distinguish the species from closely related *M. bakeri.*

Worker. Holotype: TL 5.4, HW 0.98, HL 1.03 (CI 95), ML 1.53 (MI 149), SL 1.19 (SI 122), EL 0.64, HFL 1.28 (TWI 18), WL 1.50 mm; two other workers HW 1.01 and 1.10 mm. Frontal sulcus, orbital grooves, and gap between clypeus and head capsule wide, forming conspicuous trenches bordered in black. Frontal area clearly defined. Palpal segmentation 5,4 (three inspected). Mandibles with 8 to 11 teeth and 3 to 4 preapical denticles. Either one or two apical denticles, the smallest, when present, being very minute, and the largest somewhat more massive than that of *M. bakeri.* Mandibular groove present, extending medially down shafts as described for *M. morowali.*

Shape of trunk and petiole as in *M. bakeri,* but petiolar node not as high and posterior face less steep.

Head smooth except for rugae curving above antennal bases; pronotum smooth except for a few short longitudinal rugae on anterior face extending up from neck; mesothorax with several well separated narrow longitudinal rugae laterally, and feebly granulate dorsally, with indistinct fine longitudinal rugae. Propodeum dorsally with feeble narrow transverse rugae ca. 0.01 to 0.02 mm apart which fade out on sides at about level of spiracle; declivity virtually smooth. Pilosity very dense, with more than 40 hairs breaking dorsal margin of trunk when viewed in profile. Hairs long, rising 0.13 to 0.15 mm on head and 0.18 to 0.20 mm on trunk and gaster; 3 to 4 hairs on or near each metathoracic tubercle and 8 to 11 on node of petiole. Lighter in color than other *diastematum* material, including paratype queen described below, and thus probably somewhat teneral: head orange; legs darker orange; trunk and petiole yellowish orange;

antennae and mandibles orange yellow; gaster brownish red.

Queen. Paratype with same collection number as holotype (HW 0.98) and two other Sarawak queens measured: TL 5.4 to 6.0, HW 0.98 to 1.06, HL 1.01 to 1.10 (CI 94 to 97), ML 1.43 to 1.56 (MI 141 to 142), SL 1.14 to 1.28 (SI 117 to 123), EL 0.63 to 0.68, HFL 1.23 to 1.35 (TWI 17 to 19), WL 1.50 to 1.68 mm. Mesonotum with conspicuous longitudinal rugae dorsally; remainder of trunk smooth except for feeble transverse rugae above neck on pronotum and very strongly developed transverse rugae 0.02 to 0.05 mm apart on dorsum of propodeum and extending obliquely across sides; declivitous face of propodeum smooth. Head orange red; clypeus, occipital lobe, legs and trunk reddish orange; petiole yellowish orange; antennae and mandibles orange yellow.

Paratype. One dealate queen, same date and collection number as holotype (BMNH).

Additional Records. BORNEO: *Sarawak:* Several series from 4th Division, Gunung Mulu National Park: 500 m+, pitfall trap, iv–v-1978, one worker, one dealate queen (I. Hanski, BMNH and MCZ); mixed dipterocarp forest, 2.iii.1978, leaf litter, one worker (H. Vallack, BMNH); v–viii.1978, B.M. 1978-49, camp 5, one dealate queen (P. M. Hammond and J. E. Marshall, BMNH). H. Vallack's specimen larger than holotype (HW 1.10 mm) with node of petiole somewhat taller and more massive, and with a broad shallow concavity between the propodeum and the metathoracic tubercles (but metanotal groove not visible in profile as a distinct notch).

Myrmoteras indicum new species
Figures 4, 7–10, 27, 30; Map 2

Holotype. Worker deposited in MHN from India: Tamil Nadu: Anaimalai Hills, 18 km au nord de Valparai, 1,250 m, 18.XI.1972, #35 [tamisages en forêt] (C. Besuchet and I. Löbl). Name in reference to the country of origin.

Diagnosis. The only species in the *bakeri* group from India. Workers can be distinguished from those of *M. bakeri* by having a single apical denticle and relatively slender tibiae (TWI < 21); and from *M. diastematum* by the lack of a wide sulcus between the clypeus and head capsule; and from both species by the reduced palpal segmentation (3,3 or 4,3).

Worker. Holotype (HW 1.03 mm) and four paratypes from the same locality: TL 5.3 to 5.9, HW 0.94 to 1.05, HL 1.00 to 1.12 (CI 92 to 95), ML 1.53 to 1.70 (MI 100 to 108), SL 1.18 to 1.31 (SI 124 to 127), EL 0.63 to 0.68, HFL 1.22 to 1.26 (TWI 16 to 17), WL 1.53 to 1.60 mm. Frontal sulcus conspicuous but narrow; orbital grooves moderately developed. Frontal area clearly defined. Palpal segmentation 3,3 (10 workers inspected). Mandibles with 11 to 13 teeth (usually 12) and without preapical denticles. Only one apical denticle, although this one is relatively large.

Pronotum low and evenly convex; propodeum evenly rounded, summit higher than mesothorax; metanotal groove not visible as a notch in profile. In several specimens the propodeum balloons out below the level of the spiracle (as occurs in males), but otherwise such individuals appear little different. The propodeum is more conventionally shaped in most paratypes and in all other material associated with this species. Node of petiole moderately thick; anterior face straight and vertical, posterior face less steep and curving gently into summit; summit rounded and moderately wide.

Head smooth, but some workers with traces of longitudinal rugae immediately above clypeus; pronotum smooth; mesonotum with feeble longitudinal rugae present laterally below a conspicuous ruga which extends forward from each metathoracic tubercle; mesonotum dorsally with finely transverse rugae showing traces of granulate sculpture; propodeum virtually smooth but with traces of transverse

rugae dorsally in some; remainder smooth. Pilosity sparse, with less than 10 hairs breaking dorsal margin of trunk when viewed in profile. Hairs rising 0.08 to 0.10 mm on head, trunk and gaster; zero to one hair on or near each metathoracic tubercle and two to five on node of petiole. Reddish orange head, trunk, and gaster (the latter with a touch of brown), petiole and antennae orange yellow; legs and mandibles same but lighter.

Queen. Paratypes from the type series (two measured): TL 6.2, HW 1.11, HL 1.12 to 1.15 (CI 96 to 99), ML 1.66 to 1.68 (MI 144 to 150), SL 1.31 to 1.33 (SI 118 to 120), EL 0.69 to 0.70, HFL 1.40 to 1.41 (TWI 19), WL 1.62 to 1.64 mm. Trunk smooth except for usual transverse rugae on cervix and a row of very short, feeble transverse rugae along median line dorsad on propodeum, not extending onto sides laterally (although surface sometimes indistinctly rugose below level of spiracle on sides).

Male. Paratypes from the same locality as holotype (two measured): HW 0.75, HL 0.85 to 0.86 (CI 87), SL 1.20 to 1.21 (SI 160), EL 0.43, WL 1.40 to 1.44 mm. Frontal sulcus well defined, wide near median ocellus. Scapes long, more than 1.5 × HW. Palpal segmentation same as females. Head and trunk smooth outside of conspicuous irregular rugae on cervix and on propodeum (but smooth beneath propodeal spiracle on sternites, which bulge somewhat).

Paratypes. Twenty-two workers, three alate queens, three dealate queens, and seven males, same locality and collection number as holotype (MHN, MCZ, BMNH, MCSN).

Additional Records. Unless otherwise stated, collected by C. Besuchet and I. Löbl from berlesate samples in forest habitats. INDIA: *Kerala:* Cardamom Hills, entre Pambanar et Peermade, 950 m, 9.XI.1972, #18 [près d'une rivière], seven workers, one alate queen, five dealate queens, one male (MHN, MCZ); Cardamom Hills, Valara Falls, à 46 km au sud-ouest de Munnar, 450 to 500 m, 25.XI.1972, #49 [près de la rivière], one worker, one dealate queen (MHN, MCZ); Nelliampathi Hills (nord-ouest des Anaimalai Hills), Kaikatty, 900 m, 30.XI.1972, #58 [près d'un ruisseau], thirteen workers, three alate queens, one dealate queen, six males (MHN, MCZ, MCSN). *Tamil Nadu:* Nilgiri Hills, 4,000 ft, 1907–329, one worker (H. L. Andrews, BMNH); Palni Hills, 7 km à l'est de Kodaikanal, 1,750 m, 12.XI.1972, #24, one worker (MHN); Palni Hills, 10 km au nord-ouest de Kodaikanal, 2,150 m, 15.XI.1972, #27 [lisière de forêt, avec rhododendrons et fougères, près d'une rivière], one queen (MHN); Anaimalai Hills, au-dessus d'Aliyar Dam, 1,150 m, 18.XI.1972, #34 [au pied d'un groupe d'arbres envahis par les lianes], eight workers, one alate queen, four dealate queens (MHN, MCZ, MCSN); Anaimalai Hills, Valparai, 1,100 m, 20.XI.1972, #39 [forêt avec caféiers], 17 workers (MHN, MCZ); Nilgiri Hills, 6 km à l'est de Coonoor, 1,400 m, 22.XI.1972, #42 [dans un ravin], five workers, one dealate queen, five males (MHN, MCZ); Nilgiri Hills, Coonoor, 1,600 m, 22.XI.1972, #43, five workers, three males (MHN, MCZ); Nilgiri, Hulical près de Coonoor, sur la rive droite de Coonoor River, 1,600 m, 22.XI.1972, #44 [dans un ravin], two workers, two dealate queens (MHN, MCZ).

All the material here ascribed to *M. indicum* is very similar to the type series in most respects. However, the series can be divided into two groups: all females in series 18, 39, and the queen in series 42 have a palpal segmentation of 3,3 and lack preapical denticles, as in the type series. Females in all remaining series (including workers from series 42) consistently have 4,3 palpal segmentation, and at least one (sometimes two) preapical denticles. In addition, in several series in the latter group (specifically 24, 27, 34, 49, and 58) the propodeum of the females is more or less conspicuously transversely rugose (with rugae extending obliquely over sides

and posterior declivity smooth; Figs. 7, 8); in all other series the propodeum is smooth (with traces of rugae in some queens) (Fig. 30).

Further variation between series occurs across both groups: pilosity varying from sparse to dense (with more than 20 hairs breaking dorsal margin of trunk viewed in profile in series, 18, 24, 34, and 58); zero to one hair on or near each metathoracic tubercle, or more than that number (series 18, 34, 49); frontal area not demarcated to well developed (the latter in series 34, 35, 49, and 58); variation in width of the frontal furrow; presence or absence of feeble longitudinal rugae between antennal fossae (best developed in series 58); orbital grooves moderately developed to conspicuous. Randomly selected individuals measured from all series ranged in size from 0.88 to 1.09 mm (n = 24), and CI ranged from 92 to 103 in 14 selected individuals.

Natural History and Biogeography. All collections of this species were made at altitudes between 450 and 2,150 m, suggesting *M. indicum* is restricted to higher elevations. This choice of habitat and the consequent fragmentation of the species into numbers of relatively isolated populations could account for the minor character differences between localities. That the series consistently fall out into two groups on the basis of palpal segmentation and preapical denticle number is more difficult to explain and could be evidence for the existence of two sibling species. All the series are from a relatively small area of the Western Ghats and Nilgiris, and the two groups do not separate geographically in any obvious way. The only series with representatives of both groups is #42 (from the Nilgiri Hills).

THE *DONISTHORPEI* GROUP

Size small to medium. Palpal segmentation 5,4 or 5,3. Head and trunk sculptured as in *williamsi* group, but sculpture relatively delicate. A well-marked narrow ruga which clearly originates at the base of each metathoracic tubercle extends forward across mesothorax, effectively dividing mesothorax into dorsal and lateral areas. Metanotal groove not visible as a conspicuously impressed notch in profile. Petiole distinctive: sternum highly convex beneath node (Fig. 34).

The group includes two species from Borneo, and apparently also *M. karnyi* from the Mentawai Archipelago.

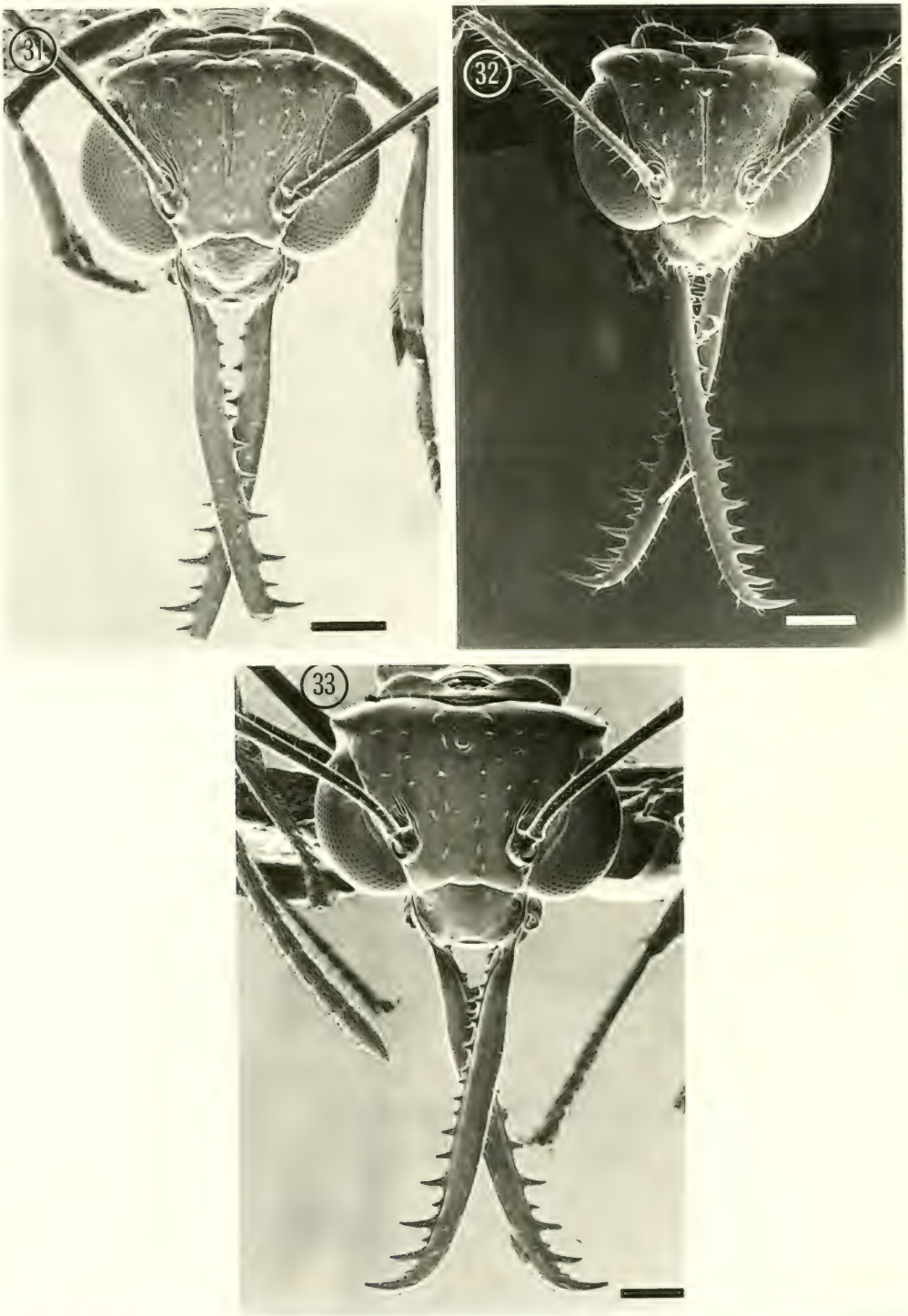
Myrmoteras chondrogastrum new species
Figures 31, 34; Map 2

Holotype. Worker deposited in BMNH from Borneo: Sarawak: 4th Division, Gunung Mulu National Park, v–viii.1978, no. 49 (P. M. Hammond and J. E. Marshall B. M. 1978). The specific name derived from Gr. *chondros* + *gaster*, referring to the granulate sculpture on the gaster.

Diagnosis. Similar to *M. donisthorpei*, but the granulate sculpture on the gaster is unique to this species.

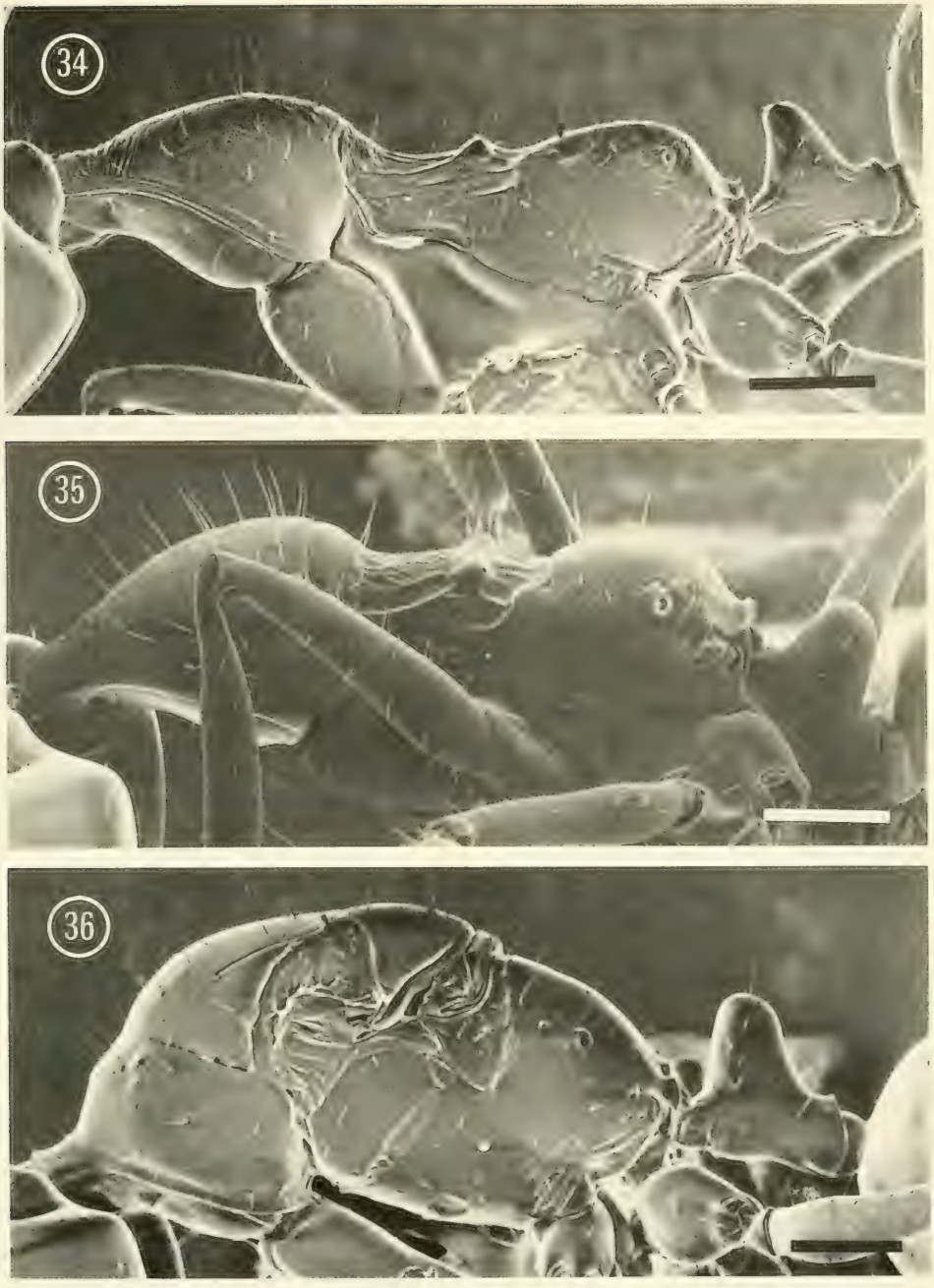
Worker. Holotype: TL 5.3 (est.), HW 0.94, HL 1.00 (CI 94), ML unknown (tips broken), SL 1.12 (SI 119), EL 0.66, HFL 1.20 (TWI 19), WL 1.45 mm. Frontal sulcus a wide trench, somewhat wider than in *M. donisthorpei* (wider midway between epistomal suture and ocelli than diameter of median ocellus); orbital furrows conspicuous. Frontal area clearly defined. Palpal segmentation 5,4. Mandibles with tips broken, probably originally with 12 teeth and 2 preapical denticles, as in queen; condition of apical denticles unknown (in the queen each mandible has a single stout apical denticle). Dorsum of mandibles with a medial groove as in *M. morowali*, but groove more feeble and extending only as far as fourth or fifth tooth from base.

Pronotum low and evenly convex; propodeum somewhat flattened dorsad, although feebly evenly convex, and with summit virtually level with mesonotum. In profile node of petiole with anterior and posterior faces straight, anterior face steep but not vertical, posterior face not as steep, curving more gently into sum-



Figures 31–33. The *donisthorpei* and *insulcatum* groups. Frontal views of the worker head. 31. *M. chondrogastrum* holotype (uncoated). 32. *M. donisthorpei* from Sarawak. 33. *M. insulcatum* (holotype queen, uncoated).

Scale lines. 0.25 mm.



Figures 34–36. The *donisthorpei* and *insulcatum* groups. Lateral views of the worker trunk and gaster. 34. *M. chondrogastrum* holotype (uncoated). 35. *M. donisthorpei* from Sarawak. 36. *M. insulcatum* (holotype queen, uncoated).

Scale lines. 0.25 mm.

mit; summit narrow. Middle and hind tibiae less dilated than in *M. donisthorpei*.

Head finely granulo-rugose, rugae between 0.01 to 0.02 mm across; posterior to median ocellus and beneath head smooth; smooth laterally except for fine vertical rugae near eyes. Frontal area and clypeus feebly granulate. Pronotum granulate, smoother laterally and with transverse rugae near neck; mesonotum with a ruga extending forward from each tubercle, very feebly granulo-rugose dorsally and longitudinally rugose laterally; dorsally propodeum with fine and very feeble transverse rugae, declivity and sides virtually smooth. Gaster very finely and irregularly granulate dorsally; laterally more feebly sculptured and smooth ventrad. Hair density moderate, with 25 hairs breaking dorsal margin of trunk when viewed in profile. Hairs short, rising 0.08 mm on head and 0.10 mm on trunk and gaster; two to five hairs on or near each metathoracic tubercle and six on node of petiole. Head orange; trunk, petiole, and mandibles orange yellow; gaster brownish orange; antennae yellowish orange; legs very light yellow.

Queen. Paratype: TL 5.6, HW 1.00, HL 1.03 (CI 97), ML 1.45 (MI 141), SL 1.15 (SI 116), EL 0.66, HFL 1.23 (TWI 18), WL 1.48 mm. Trunk dorsally with feeble granulate sculpture, tending towards longitudinally granulo-rugose medially on mesonotum; smooth laterally. Propodeum transversely rugose dorsally and obliquely rugose on sides, rugae ca. 0.15 mm apart; declivity smooth.

Paratype. Single dealate queen, same date and collection number as holotype (MCZ).

Additional Records. Known only from type series.

Myrmoteras donisthorpei
Figures 32, 35; Map 2

Myrmoteras donisthorpei Wheeler, 1916: 14, fig. 3. Borneo: West Sarawak: Mt. Matang, 16.1.1914, 1 alate queen (G. E. Bryant, MCZ [examined]). Emery, 1925: pl. 1, fig. 16. Creighton, 1930: 187, pl. 11, fig. 3.

Diagnosis. With the distinguishing characteristics of the *donisthorpei* group and a smooth and shining gaster, and with summit of propodeum not higher than the mesonotum.

Worker. Described for the first time from several series from Borneo. TL 4.5 to 4.8, HW 0.83 to 0.90, HL 0.82 to 0.91 (CI 97 to 101), ML 1.20 to 1.38 (MI 146 to 154), SL 0.84 to 0.98 (SI 102 to 109), EL 0.56 to 0.61, HFL 0.83 to 0.95 (TWI 24 to 27), WL 1.19 to 1.28 mm. Frontal sulcus a narrow groove; orbital furrow moderately conspicuous. Frontal area present but poorly demarcated. Palpal segmentation 5,4 in two workers from Sarawak and 5,3 in the worker from Sabah. Workers from Sarawak and Sabah with 12 to 13 teeth and 2 to 4 preapical denticles (usually 2 to 3); single worker from Kalimantan with 10 teeth and 3 preapical denticles on both mandibles. Apical denticle pair small in size, the smallest very tiny and closely applied to the slender, more apical denticle.

Trunk as described for *M. chondrogastrum* except in side view with a wide, shallow concavity between metathoracic tubercles and propodeum (but metanotal groove not visible as a conspicuously impressed notch in profile). Petiole also very similar, but with anterior face of node closer to vertical; summit broader. Tibiae strongly dilated.

Head (including frontal area and clypeus) longitudinally granulo-rugose, with sculpture extending back to about as far as median ocellus, rugae ca. 0.01 mm across; smooth on occiput, laterally beneath eyes (except for feeble vertical rugae near eyes) and under head. Pronotum transversely granulo-rugose, sculptured more feebly on sides; mesothorax longitudinally granulo-rugose dorsad, laterally with three to five narrow longitudinal rugae on smooth surface; propodeum feebly granulate, declivity very feebly trans-

versely granulo-rugose to smooth. Hair density moderate, with 17 to 26 hairs breaking dorsal margin of trunk when viewed in profile. Hairs short, rising 0.06 to 0.08 mm on head and 0.10 mm on trunk and gaster; two to three hairs on or near each metathoracic tubercle and five to seven on node of petiole. Mostly orange red to reddish orange, with head slightly lighter colored and legs reddish orange with femora, trochanters, and sometimes the coxae virtually white; antennae and mandibles orange yellow. Sabah specimen very dark orange red, including legs.

Queen. Holotype: TL 4.5, HW 0.85, HL 0.88 (CI 97), ML 1.26 (MI 144), SL 0.91 (SI 107), EL 0.58, HFL 0.88 (TWI 24), WL 1.20 mm. Both mandibles with 12 teeth and two preapical denticles (Sarawak queen with 11 to 12 teeth). Less strongly sculptured than described for Sarawak workers, with sculpture on head rugulose, rugae ca. 0.01 mm in width; clypeus more feebly and irregularly rugulose; trunk virtually smooth, very feebly granulate on mesonotum; propodeum transversely rugose dorsally (rugae 0.02 to 0.03 mm apart), obliquely rugose on sides, and with declivity virtually smooth. Coloration similar to workers but femora not as pale.

Male. Described for the first time from a Sarawak specimen: HW 0.59, HL 0.65 (CI 91), SL 0.78 (SI 132), EL 0.34, WL 0.98 mm. Frontal sulcus a feebly impressed medial line. Papal segmentation 6,4. Head smooth except for a trace of granulate sculpture low on face; clypeus feebly granulate. Trunk granulate; propodeum with a denser network of rugae than in *M. williamsi*; these continue onto declivity. Traces of granulate sculpture on petiole.

Additional Records. BORNEO: *Sarawak:* 4th Div., Gunung Mulu National Park, v–viii 1978, B. M. 1978-49, camp 1 [three workers, one dealate queen, one male]; camp 5 [one worker] (P. M. Hammond and J. E. Marshall, BMNH and MCZ); ibid., limestone forest, 27.v.78 pitfall trap, one worker (H. Vallack, BMNH). *Sabah:* Gunung Silam 880 m, 1983, A19 9.2, one worker (R. Leakey, BMNH). S. *E. Kalimantan:* 17-46 km W Batulitjin, 28 June–2 July 1972, lowland rainforest, soil under litter, one worker (W. L. Brown, MCZ). Queen from Batulitjin (HW 0.92) larger than holotype but likewise with measurements and indices within range shown by the workers; sculpturing stronger than holotype: head granulo-rugose, pronotum, mesonotum, and scutellum granulate.

Myrmoteras karnyi

Map 2

Myrmoteras karnyi Gregg, 1954: 23, fig. 1. Indonesia: Mentawai Archipelago: Sipora Island, 22G, 31 October 1924 (H. H. Karny. Deposited in Zoologisch Museum en Laboratorium, Bogor; holotype not found).

Diagnosis. Apparently similar to *donisthorpei*, but with pronotum and propodeum relatively very high and convex: summit of propodeum higher than mesonotum, and as high as summit of pronotum.

Worker. No specimens seen. Can be assigned to *Myagroteras* from examination of figure in Gregg (1954), which is relatively detailed and is assumed to be accurate. The figure shows a conspicuous frontal sulcus, mandibles only very feebly curving ventrad near tips, and the lack of trigger hairs and projecting triangular labrum. I tentatively place *M. karnyi* in the *donisthorpei* group because of the strong convex curvature of the sternum of the petiole, as judged by the illustration of Gregg (1954). Also the sculpture, although apparently not granulate as in the other species in this group, is much better developed than in species of the *bakeri* group. However, the conformation of the trunk apparently bears a resemblance to *M. williamsi*, and it is possible that *karnyi* belongs in the *williamsi* group.

Figure 37. Labral structure, *M. insulcatum* (uncoated holotype). Arrow indicates one of the long labral hairs. *Scale line.* 0.05 mm.

The following is based on the description of Gregg and the figure which accompanies it: frontal furrow a narrow, conspicuous groove; orbital furrows narrow, moderately conspicuous (in drawing appearing much as in *donisthorpei*). Mandibles with 10 teeth and two apical denticles, but apparently lacking preapical denticles. Head dorsally with narrow longitudinal "striations or rugulae" from

margin of clypeus to well above antennal bases, behind this apparently smooth; rugae straight except where they curve around the antennal insertions. Pronotum higher and more strongly convex than in *M. donisthorpei* and *chondrogastrum*; mesothorax with "strong longitudinal rugae," and strongly depressed relative to pronotum and propodeum, "recalling the condition in *williamsi*"; propodeum as high as the pronotum and strongly convex, and from drawing apparently longitudinally rugose. Pilosity on trunk apparently at least moderately dense. Petiole strongly convex beneath node; node apparently narrower than in *donisthorpei* or *chondrogastrum*. Middle and hind tibiae relatively slender, with the drawing comparing favorably with *chondrogastrum*, and unlike the strongly dilated condition in *donisthorpei*. Color unknown.

Length in original description given as 3.6 mm. However, judging from the value Gregg gives for the length of the *M. ceylonicum* holotype (Gregg, 1956), his measure of total length does not include ML; TL therefore estimated as 4.5 to 4.6 mm. "Head index" given as 0.92, but the value of this index given by Gregg (1956) for *ceylonicum* holotype is much lower than that calculated given the definition of cephalic index used here; calculation based on Gregg's illustration of *karnyi* yields a CI of 97. These estimates of the TL and CI values compare very favorably to the values for *M. donisthorpei*.

THE *INSULCATUM* GROUP

Head and trunk highly polished, lacking sculpture. No trace of frontal sulcus on head (sulcus conspicuous in all other species in the subgenus). Clypeus only feebly convex medially, as in most species in the subgenus *Myrmoteras*. The two labral hairs presumed homologous with the trigger hairs of the subgenus *Myrmoteras* are more widely separated than in any other species of *Myagroteras* (Fig. 37). Palpal segmentation 3,3. Mandibles with 14 to 15 teeth, the highest number recorded.

Known only from a single dealate queen from the Philippines.

Myrmoteras insulcatum new species
Figures 33, 36, 37; Map 2

Holotype. Dealate queen deposited in MCZ from Philippines: Luzon: Lagunas: Mt. Makiling, ca. 150 m below summit, litter, Feb. 1968 (R. A. Morse). Name from Latin *in* + *sulcus*, referring to the lack of a frontal sulcus.

Diagnosis. The only species of *Myagroteras* completely lacking a frontal sulcus.

Queen. Holotype: TL 5.6, HW 1.07, HL 1.01 (CI 106), ML 1.53 (MI 152), SL 1.08 (SI 100), EL 0.61, HFL 1.16 (TWI 22), WL 1.54 mm. Orbital grooves moderately developed. Frontal area present but somewhat poorly demarcated. Palpal formula 3,3. Mandibles with 14 to 15 teeth and two preapical denticles. Apical denticles both tiny, the smallest very tiny and closely applied to the larger, which is closely applied in turn to the apical tooth. A feeble groove extends longitudinally down the dorsal surface of mandible to at least penultimate tooth, but unlike other ants with such a groove (*M. morowali, diastematum*, and some *bakeri*), the groove extends very close to inner, toothed margin (Fig. 37).

Node of petiole with straight, nearly vertical anterior face, posterior face steep

→

Figures 38–41. The *williamsi* group. Frontal views of the worker head. 38. *M. morowali* paratype (arrows indicate postocular distance). 39. *M. toro* paratype. 40. *M. williamsi* (from Negros; specimen oily). 41. *M. wolasi* holotype (uncoated).

Scale lines. 0.25 mm.

Figures 42–45. The *williamsi* group. Lateral views of the worker trunk and gaster. 42. *M. morowali* paratype (arrow indicates location of metanotal groove). 43. *M. toro* paratype. 44. *M. williamsi* (from Negros; specimen oily). 45. *M. wolasi* holotype (uncoated).

Scale lines. 0.25 mm.

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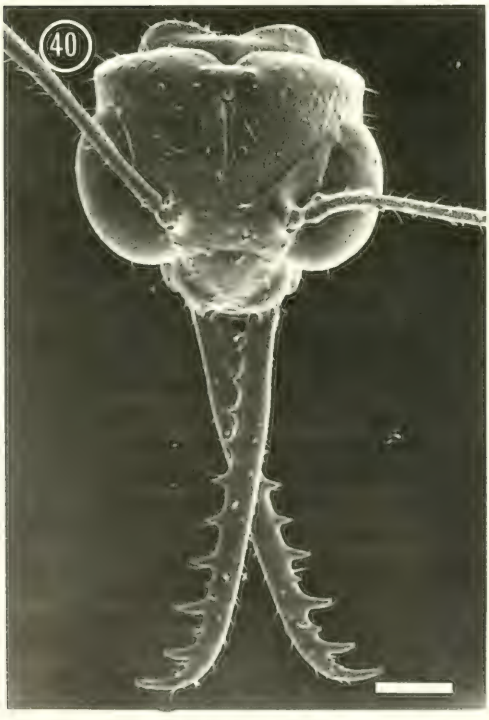
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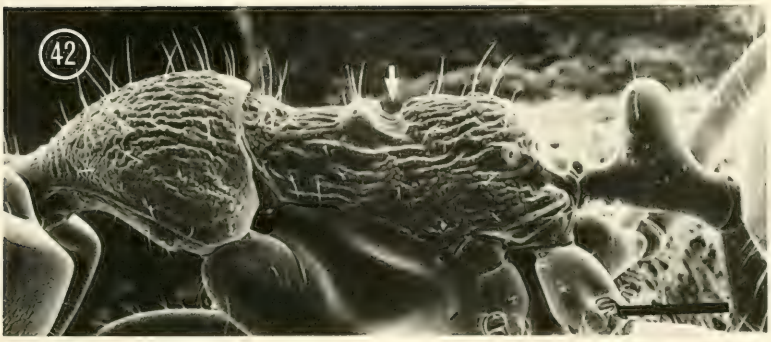
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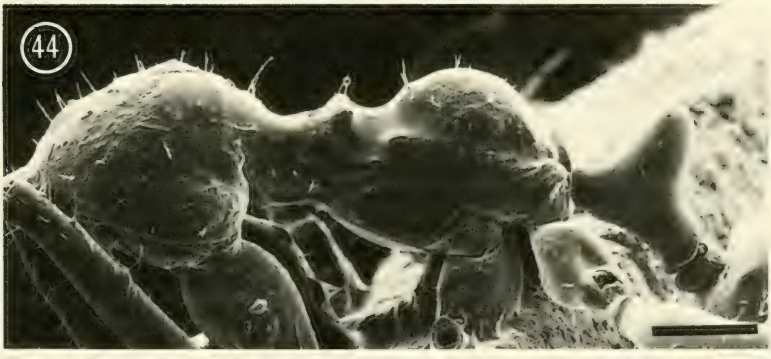
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and curving; summit wide and rounded. Ventral margin of petiole feebly convex beneath node.

Head, trunk and gaster entirely smooth and very highly polished. Hair density moderate; hairs short and moderately abundant, rising 0.08 mm on head, 0.14 mm on trunk and gaster; eight hairs on node of petiole. Dark orange red, with clypeus and occipital lobe somewhat lighter, mandibles orange yellow, legs and antennae reddish orange.

Additional Records. Known only from holotype.

The *williamsi* Group

Size small to medium (known range of females: TL 4.2 to 5.0 mm, except *M. toro* 5.2 to 5.6 mm). Head and pronotum strongly granulate or granulo-rugose. Orbital grooves moderately developed, less conspicuous than in other *Myagroteras* species. Postocular distance at least 20% of eye length (narrower in all other species in the genus). Palpal segmentation 6,4 (at least two workers in each species inspected where available). Lacking a conspicuous narrow ruga extending forward along sides of mesonotum from base of each metathoracic tubercle. Metanotal groove usually conspicuously impressed. Sternum of petiole feebly convex beneath node.

This group includes three closely related species from Sulawesi, all of which are new. These represent the first records of the genus *Myrmoteras* for Sulawesi, which now is the farthest the genus is known to extend to the southeast. In addition, I include here the distinctive Philippine species *M. williamsi*.

Myrmoteras morowali new species
Figures 38, 42; Map 2

Holotype. Worker deposited in BMNH from Indonesia: Central Sulawesi: near Morowali, Ranu river area, 27.i.–20.iv.1980, B.M. 1980–280 (M. J. D. Brendell). Name is a noun in apposition after the type locality.

Diagnosis. Distinguished from closely related *M. wolasi* and *M. toro* by the finely granulate sculpture dorsally on head and pronotum; very smooth and shining frontal area; granulate clypeus; presence of transverse rugae across declivity of propodeum, which is smooth only near base; and light yellow color, with the petiole concolorous with trunk and gaster.

Worker. Holotype (HW 0.80) and four paratypes: TL 4.2 to 4.5, HW 0.80 to 0.82, HL 0.83 to 0.85 (CI 96 to 97), ML 1.13 to 1.19 (MI 140 to 144), SL 0.87 to 0.90 (SI 108 to 112), EL 0.49 to 0.50, HFL 0.87 to 0.93 (TWI 22 to 23), WL 1.15 to 1.20 mm. Frontal sulcus a very narrow, well-defined groove. Frontal area very clearly defined. Mandibles with 11 to 12 teeth (usually 11) and two to four preapical denticles (usually three). Smallest apical denticle tiny, closely applied to the larger denticle, which is small and sharp. Mandibles with feeble but conspicuous medial grooves extending longitudinally for most of the length of the shafts (absent in *M. wolasi*).

Trunk very similar to *M. toro*, except propodeum dorsally flattened and with posterior slope of petiole relatively straight, curving only at base and summit. Metanotal groove conspicuously impressed but narrower than in *M. toro*.

Finely and regularly granulate dorsally on head and clypeus, also granulate (but more feebly) on back of head, including occipital lobe; granules ca. 0.01 mm across. Frontal area smooth and translucent, and thus standing out prominently. Sides of head below eyes longitudinally granulo-rugose; ventral surface of head smooth. Pronotum granulate, granules formed into broad longitudinal rugae, particularly dorsad; mesonotum densely longitudinally rugose, with traces of granulate sculpture, pleura of mesothorax with similar, but less dense rugae, granulate sculpture absent; propodeum with longitudinal granulate rugae, declivity transversely rugose except near base. Pilosity dense, with 30 to 36 hairs breaking dorsal margin of trunk in profile. Hairs short, rising to 0.06 to 0.08 mm on head and 0.10 mm on trunk and gaster. Two or three hairs at or near each metathoracic tubercle; node of peti-

ole with four to eight hairs. Color exceptionally light, uniform yellow or orange yellow, mandibles somewhat lighter.

Queen. TL 4.5, HW 0.80, HL 0.83 (CI 97), ML 1.13 (MI 137), SL 0.86 (SI 107), EL 0.48, HFL 0.90 (TWI 22), WL 1.21 mm. Dorsum of trunk granulate, with the mesonotum and scutellum longitudinally granulo-rugose; mesepisternum much smoother; propodeum with strong narrow transverse rugae 0.02 to 0.03 mm apart, smooth low on declivity. Uniform yellowish orange.

Paratypes. One dealate queen and four worker paratypes with same locality data and collection number (BMNH and MCZ).

Additional Records. Known only from type series.

Myrmoteras toro new species
Figures 1, 39, 43, 46, 47; Map 2

Holotype. Worker deposited in MCZ from Indonesia: Central Sulawesi: Lore Lindu National Park at Toro, 82 km south of Palu, disturbed rainforest, single cluster of ants in loose leaf litter, 15.VII.1983 (M. W. Moffett). The specific name is a noun in apposition after the type locality.

Diagnosis. Can be distinguished from *M. wolasi* and *morowali* by its larger size, the lack of granulate sculpture on the clypeus, and the relatively more rounded propodeum.

Worker. Holotype (HW 1.01 mm) and paratypes: TL 5.2 to 5.6, HW 0.97 to 1.05, HL 0.97 to 1.03 (CI 100 to 102), ML 1.48 to 1.58 (MI 153 to 154), SL 1.07 to 1.15 (SI 109 to 110), EL 0.58 to 0.62, HFL 1.13 to 1.18 (TWI 19 to 22), WL 1.35 to 1.56 mm (eight measured). A medium-sized species. Frontal sulcus narrow (0.01 to 0.02 mm wide), anterior to antennal bases weak and difficult to distinguish from the heavy sculpturing. Frontal area poorly demarcated, unlike *M. morowali.* Mandibles with 11 to 13 teeth (usually 12) and two to three preapical denticles. Apical denticles tiny and not greatly different in size; the most apical is closely applied to the apical tooth. Mandibles dorsally without any trace of feeble grooves found in *M. wolasi.*

Pronotum low and convex; propodeum evenly convex (except for somewhat abrupt declivity), summit virtually level with mesonotum. Metanotal groove conspicuously impressed. Node of petiole with vertical anterior slope and steep but more curving posterior slope; node narrow. Petiole feebly convex beneath node.

Dorsum of head densely packed with very wavy, ca. 0.02 mm wide rugae, which encircle antennal bases and proceed otherwise more or less longitudinally; back of head (behind ocelli) feebly rugulose, with rugae radiating out from along dorsal and lateral margins of occipital lobe, and with similar rugae on the lobe itself, particularly mesad; clypeus with feeble longitudinal rugae laterally, smoother medially, without granulate sculpture; frontal area feebly irregular. Finely longitudinally rugose on sides below eyes; smooth beneath head. Pronotum with very irregular, sinuous rugae, thicker and more widely separated than those on head. Mesothorax and propodeum with rugae ca. 0.03 to 0.04 mm apart, these mostly more or less longitudinal (oblique laterally on mesothorax), katepisternum, mesonotum, and dorsum of propodeum with rugae less distinct; declivity of propodeum with irregular transverse rugae near summit, below that virtually smooth. Pilosity very dense, with more than 40 hairs breaking dorsal margin of trunk when viewed in profile. Hairs rising 0.10 to 0.12 mm on head, trunk and gaster; two to three hairs on or near each metathoracic tubercle and five to nine on node of petiole. Most workers uniformly very dark orange red; mandibles, tarsi, and trochanters yellowish orange. Two teneral individuals have orange yellow to reddish yellow heads, trunks and legs, gasters brownish orange, and antennae, mandibles, trochanters and tarsi orange yellow.

Queen. See Figure 46. TL 5.5, HW 1.03, and other measurements within the range shown by workers. Dorsum of trunk granulate, with the mesonotum and scutellum longitudinally granulo-rugose; pleura relatively smooth; propodeum transversely rugose.

Paratypes. Workers and dealate queen from same colony (MCZ, BMNH, MHN, MCSN).

Additional Records. Known only from type series.

Natural History. The type series apparently represents a complete colony consisting of 22 workers and one queen, which was collected between loose leaves in the leaf litter on the forest floor. In captivity the ants foraged solitarily for various soft bodied invertebrate prey, which they captured with their trap-like jaws (Fig. 47).

Myrmoteras williamsi
Figures 40, 44; Map 2

Myrmoteras williamsi Wheeler, 1919: 146. Philippine Islands: Luzon: Los Baños, 2 alate queens, 1 male (F. X. Williams, MCZ, queens examined, male missing). Creighton, 1930: 189, fig. 2, pl. 11, fig. 4, worker described.

Diagnosis. Shape of the trunk in workers distinctive: pronotum and propodeum high and strongly convex; mesothorax relatively depressed. *M. williamsi* has only been collected in the Philippines. *M. karnyi* (tentatively placed in the *donisthorpei* group) has a somewhat similarly shaped trunk, but the head and trunk of this species are apparently not strongly granulate (Gregg, 1954).

Workers. Known only from Negros. Two measured (numbers in brackets indicate measurements that could only be taken on the smaller specimen): TL [5.0], HW 0.95 to 1.00, HL 0.95 to 1.00 (CI 100), ML 1.38 to 1.50 (MI 145 to 151), SL [1.10] (SI [113]), EL 0.55 to 0.58, HFL 1.05 to 1.18 (TWI [21]), WL 1.30 to 1.40 mm. Frontal sulcus very narrow but well defined. Frontal area present but poorly demarcated. Clypeus less strongly convex medially than in most other *Myagroteras* species, although not as flattened as in most *Myrmoteras*. Palpal segmentation 6,4 (two workers inspected). Mandibles with 11 to 13 teeth and two preapical denticles. Apical denticles small, the smallest tiny, but conspicuous, the largest closely applied to apical tooth for much of its length. Mandibles bent more strongly ventrad at penultimate tooth than in other *Myagroteras*, but not as strongly as in subgenus *Myrmoteras*.

Both pronotum and propodeum very high and rounded (except declivity of propodeum virtually straight), so that mesonotum appears relatively very depressed. In profile with a wide concavity between metathoracic tubercles and propodeum, but metanotal groove not visible as a conspicuously impressed notch in profile. Petiole with steep to nearly vertical anterior slope; posterior slope less steep, straight but curving gently up to summit.

Head (including frontal area and clypeus), pronotum and propodeum finely and evenly granulate, granules 0.01 to 0.02 mm across, present as well on back of head and laterally beneath eyes, and with traces of granular sculpture beneath head; declivity of propodeum smooth; mesothorax with feeble granulate sculpture, widely separated narrow longitudinal rugae on sides and virtually smooth above; funiculi, mandibles and legs feebly granulate, with the sculpture strongest on the tibiae; petiole and gaster smooth. Pilosity sparse to moderate, with 6 to 18 hairs breaking dorsal margin of trunk when viewed in profile (but specimens in very poor condition and conceivably have lost hairs). Hairs short, rising 0.06 mm on head, trunk and gaster; one to two hairs on or near each metathoracic tubercle and two to three on node of petiole. Head and trunk reddish orange (except clypeus and occiput orange red); petiole same but slightly lighter; gaster brownish or yellowish orange; legs yellowish orange; mandibles and antennae orange yellow.

Queen. Syntypes (two measured): TL 4.4 to 5.0, HW 0.91 to 0.96, HL 0.88 to 0.93 (CI 103), ML 1.15 to 1.18 (MI 127 to 130), SL 0.91 to 0.94 (SI 99 to 100), EL 0.53 to 0.56,. HFL 0.89 to 1.00 (TWI 19 to 22), WL 1.18 to 1.28 mm. Hairs moderately dense and longer than in Dumaguete worker specimens (0.08 to 0.10 mm). Trunk finely and evenly granulate, pro-

Figures 46–47. *Myrmoteras toro* paratypes. 46. Queen. 47. Forager carrying a mosquito, which it had captured after the author dropped the prey, wounded, in front of it.

podeum transversely granulo-rugose, including on declivity. Funiculi, mandibles and legs smooth.

Male. Single male from Mt. Makiling: HW 0.68, HL 0.75 (CI 91), SL 0.84 (SI 124), EL 0.38, WL 1.2 mm. Frontal sulcus a shallow groove beginning well above clypeus and ending before reaching median ocellus. Maxillary palpi with six segments. Head and trunk granulate; longitudinally granulo-rugose dorsad on mesonotum, more feebly granulate laterally; propodeum feebly granulate with a conspicuous network of raised ridges, except declivity virtually bare outside of medial ruga.

Additional Records. PHILIPPINES: *Luzon:* Benguet, Baguio, one alate queen (C. F. Baker, BMNH); Mt. Makiling, one alate queen, one male (C. F. Baker, BMNH and MCZ). *Negros Oriental:* Dumaguete: Camp 4.6.1927; Camp 4.2.1931; Lake 4.30.1931 [each with one worker] and 5.18.1927 [one dealate queen] (J. W. Chapman, MCZ). Specimens from Negros have relatively longer mandibles (MI 139 to 151, compared with 124 to 130 for Luzon specimens) and scapes (SI 110 to 111 compared with 99 to 100). Also, the Negros specimens have a feeble granulate sculpture on the legs, scapes, and mandibles lacking in Luzon material. Negros queen with propodeum more evenly granulate than in types (granules only feebly arranged in transverse rugae); declivity of propodeum smooth near base.

Natural History. Little is known, but J. W. Chapman (in Creighton, 1930) indicated that the ants are "slow and clumsy in movement." F. X. Williams (in Wheeler, 1922) reported that the species nests in the soil.

Myrmoteras wolasi new species
Figures 41, 45; Map 2

Holotype. Worker deposited in MCZ from Indonesia: S.E. Sulawesi: rainforest 1–2 km east of Wolasi, 42 km south of Kendari, ca. 350 m, 13–14 July 1972 (W. L. Brown). The specific name is a noun in apposition after the type locality.

Diagnosis. Distinguished from *M. morowali* and *M. toro* by the presence of distinct granulate sculpture on both the clypeus and frontal area (head and pronotum otherwise conspicuously rugose); declivity of propodeum entirely smooth; and color darker, with petiole strikingly lighter in color than trunk or gaster. Also distinguished from *M. toro* by its smaller size and dorsally flattened propodeum.

Worker. Holotype: TL 4.5, HW 0.88, HL 0.88 (CI 100), ML 1.23 (MI 141), SL 0.96 (SI 109), EL 0.55, HFL 0.98 (TWI 21), WL 1.20. Frontal sulcus a narrow groove, and, like orbital grooves, somewhat wider and more conspicuous than in *M. toro.* Frontal area clearly defined. Both mandibles with 12 teeth and two denticles. Apical denticles both tiny, with little difference in size as in *M. toro.* Mandibles dorsally without any trace of the feeble medial grooves found in *M. morowali.*

Shape and conformation of trunk and petiole exactly as described for *M. morowali,* but with node of petiole narrower.

Sculpture on head similar to *M. toro,* but with rugae wider, 0.03 mm across; rugae longitudinal but diverging somewhat towards occiput. Clypeus and frontal area evenly granulate throughout, not rugose; granules ca. 0.01 mm wide. Back of head smooth except for a few rugae directly behind ocelli; feebly rugulose on occipital lobe as in *M. toro.* Fine longitudinal rugae on sides below eyes; smooth beneath head. Pronotum similar to *M. toro,* with rugae like those on head but more sinuous, mostly transverse caudad and mostly longitudinal farther back and on sides; mesothorax and propodeum rugose as described for *M. toro,* but with declivity entirely smooth. Pilosity very dense, as described for *M. toro.* Head and trunk orange red, petiole (as well as legs and antennae) contrasting yellowish orange, tarsi and mandibles orange yellow.

Additional Records. Known only from holotype.

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LITERATURE CITED

BINGHAM, C. T. 1903. Hymenoptera. Vol. 2. Ants and cuckoo-wasps. *In* W. T. Blanford (ed.), Fauna of British India, including Ceylon and India. Taylor and Francis, London, xix + 506 pp, 1 pl.

BROWN, W. L., JR., AND W. L. NUTTING. 1949. Wing venation and the phylogeny of the Formicidae (Hymenoptera). Trans. Amer. Ent. Soc., **75:** 113–131, pl. 8–9.

CARLIN, N. C. 1983. Polymorphism and division of labor in the dacetine ant *Orectognathus versicolor* (Hymenoptera: Formicidae). Psyche, **88**(3–4): 231–244.

CREIGHTON, W. S. 1930. A review of the genus *Myrmoteras* (Hymenoptera: Formicidae). J. N.Y. Ent. Soc., **38:** 177–192, 1 pl.

EISNER, T. 1957. A comparative morphological study of the proventriculus of ants (Hymenoptera: Formicidae). Bull. Mus. Comp. Zool., **116**(8): 439–490, pl. 1–25.

EMERY, C. 1925. Hymenoptera. Family Formicidae, subfamily Formicinae. *In* P.Wytsman (ed.), Genera Insectorum, fasc. 183. V. Verteneuil and L. Desmet, Brussels, 302 pp., 4 pl.

FARRIS, J. S. 1970. Methods for computing Wagner trees. Syst. Zool., **19:** 83–92.

FELSENSTEIN, J. 1982. Numerical methods for inferring evolutionary trees. Q. Rev. Biol., **57:** 379–404.

FOREL, A. 1893. Note preventive sur un nouveau genre et une nouvelle espèce de Formicide. Ann. Soc. Ent. Belg., **37:** 607–608.

———. 1894. Formicides de l'empire des Indes et de Ceylon. J. Bombay Nat. Hist. Soc., **8:** 419.

GOTWALD, W. H., JR. 1969. Comparative morphological studies of the ants, with particular reference to the mouthparts (Hymenoptera: Formicidae). Cornell Exper. Station Memoir 408, 150 pp.

———. 1973. Mouthpart morphology of the African ant *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae). J. N.Y. Ent. Soc., **81**(2): 72–78.

GREGG, R. E. 1954. Geographical distribution of the genus *Myrmoteras*, including the description of a new species (Hymenoptera: Formicidae). Psyche, **61**(1): 20–30.

———. 1956. A new species of *Myrmoteras* from Ceylon (Hymenoptera: Formicidae). Psyche, **63**(2): 41–45.

HARRIS, R. A. 1979. A glossary of surface sculpturing. Occasional papers in entomology, California Dept. Food and Agriculture, No. 28, 31 pp.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool., **33**(1): 83–103.

WHEELER, W. M. 1916. Four new and interesting ants from Borneo and Luzon. Proc. New England Zool. Club, **6**: 9–18.

———. 1919. The ants of Borneo. Bull. Mus. Comp. Zool., **63**(3): 43–147.

———. 1922. Observations on *Gigantiops destructor* Fabricius and other leaping ants. Biol. Bull., **42**(4): 185–201.

———. 1933. A new *Myrmoteras* from Java. Proc. New England Zool. Club, **13:** 73–75.

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Revision of the Myrmicine Genus *Acanthomyrmex* (Hymenoptera: Formicidae)

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REVISION OF THE MYRMICINE GENUS *ACANTHOMYRMEX* (HYMENOPTERA: FORMICIDAE)

MARK W. MOFFETT[1]

ABSTRACT. The myrmicine genus *Acanthomyrmex* is revised in full. Eleven species of these dimorphic Asian ants are described, including six new species (*A. basispinosus, careoscrobis, concavus, foveolatus, laevis,* and *mindanao*). I distinguish two species groups, the *luciolae* group with six species and the *notabilis* group, with five. This informal division is supported by a cladistic analysis.

INTRODUCTION

Acanthomyrmex ants are endemic to Southeast Asia, including Sri Lanka (but as yet none have been recorded from India or New Guinea); the ants have very small colonies and are seldom collected (Moffett, 1985). I provide descriptions of the first new species of this genus to be recognized in a half century, and divide the species into two species groups. A cladistic analysis provides preliminary information regarding evolution within the genus.

All *Acanthomyrmex* species are dimorphic, with the genus including the most impressive examples of allometric growth known for the workers of ants. As an example, a major of *A. notabilis* selected from a Sulawesi series has a head length twice that of a minor worker from the same nest; because of differences in head shape, the cephalic volume is roughly ten times greater. Yet the major's antennae are only 5% longer than those of the same minor, while its trunk is only 3% longer, and roughly has a volume only 6% greater; furthermore, the body length of the minor (trunk length + petiole length + postpetiole length + gaster length) is slightly larger than that of the major. The result is a major caste so absurdly proportioned that seen from certain angles live individuals appear to consist of little more than a head. Behavioral information on *Acanthomyrmex notabilis* and *A. ferox* (from the *notabilis* and *luciolae* species groups, respectively) indicates the majors serve roles in nest defense, and presumably also mill the seeds which apparently form a large part of the diet of these omnivores; in addition, majors occasionally participate in brood care (Moffett, 1985).

RELATIONSHIPS

The relationships between *Acanthomyrmex* species were studied using the program PAUP (version 2.3), written by David L. Swofford.

Character Coding for Computer Analysis

The characters and character state codes used in cladistic analysis are defined in the following section on terminology; the character states for each species and two possible outgroups are given in Table 1. The characters numbered 41 through 44 in Table 1 were of no value in determining species relationships and thus were excluded from the cladistic analysis. All characters were treated as binary or ordered. Polymorphism in a species (whether within or between series) was treated as if the data were missing for that species. Range limits for numerical characters

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TABLE 1. DATA MATRIX OF MORPHOLOGICAL CHARACTERISTICS FOR SPECIES OF *ACANTHOMYRMEX* AND TWO HYPOTHETICAL OUTGROUPS.†

Taxon	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
OUTGROUP																		
MYRMECININI	0–1	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?	?	?
TETHEPA	1–2	?	0	?	?	?	?	?	1	?	?	?	?	?	?	1	?	0
LUCIOLAE GROUP																		
A. basispinosus	2	0	1	1	1	0	0	0	0	1	0	2	1	1	P	P	1	1
A. crassispina	1	0	P	0	0	0	1	1	2	P	1	1	0	0	0	0	0	1
A. dusun	?	0	?	?	0	0	?	0	?	1	1	1	?	1	1	?	?	?
A. ferox	0	0	0	1	P	1	P	0	0	1	0	0	0	1	0	0	0	0
A. laevis	0	?	0	?	?	?	1	?	0	?	?	?	0	?	0	0	0	0
A. luciolae	2	0	0	1	1	1	0	0	1	1	0	0	0	1	0	0	P	1
NOTABILIS GROUP																		
A. careoscrobis	1	?	0	0	?	?	1	?	1	?	?	?	0	?	1	0	P	1
A. concavus	2	?	1	0	?	?	P	?	2	?	?	?	0	?	1	1	1	0
A. foveolatus	?	1	?	?	0	0	?	1	?	0	P	2	?	0	1	?	?	?
A. mindanao	1	1	1	0	0	0	1	0	1	0	1	2	0	1	1	1	0	P
A. notabilis	0	1	0	0	1	0	P	0	0–1	P	P	2	1	1	P	0	1	0

† In the table "?" refers to missing data and "P" refers to a polymorphic condition, or an intermediate condition, as discussed in the text. Character numbers refer to the characters that follow: 1. minor head shape; 2. major head shape; 3. minor greatest head width; 4. minor cephalic sculpture; 5. major foveate sculpture; 6. major rugose sculpture; 7. minor pilosity height; 8. major pilosity density; 9. CI (minors); 10. CI (majors); 11. cephalic hollow; 12. darkly pigmented medial streak; 13. frontal sulcus (minors); 14. frontal sulcus (majors); 15. clypeal index; 16. medial clypeal lobes; 17. lateral clypeal hairs; 18. clypeal rugae; 19. medial projection; 20. SI; 21. funicular index; 22. propodeal spine length; 23. pronotal spine length; 24. pronotal angle; 25. propodeal declivity; 26. propodeal spiracle diameter; 27. petiolar spines; 28. PWI; 29. subpetiolar declivity; 30. anterior petiolar peduncle length; 31. petiolar index; 32. lateral petiolar hair; 33. sublateral petiolar hair; 34. postpetiole narrowness; 35. postpetiole node; 36. postpetiole pilosity; 37. gaster pilosity; 38. femur concavity; 39. femur pilosity; 40. FLI; 41. FWI; 42. pronotal spine pilosity; 43. hypostomal teeth; 44. ventral mandible tooth.

were chosen to cleanly separate the maximum number of species; species were considered polymorphic when the values for a numerical character were spread on either side of these limits, or when the species was known from only the holotype and the value for that specimen was near to the limit. As more *Acanthomyrmex* material becomes available, it will become easier to evaluate characters for their usefulness in phylogenetic studies.

OUTGROUPS

The affinities of *Acanthomyrmex* are uncertain. Emery (1922) placed the genus in a subtribe of the Myrmecinini along with *Pristomyrmex*, *Myrmecina* and *Dacryon*, because in these genera the lateral portions of the clypeus form only a thin transverse ridge anterior to the antennal fossae (Fig. 1). In other myrmecinine genera the clypeus is thicker and wider laterally. However, he was unable to provide any certain characters which uniquely define the Myrmecinini as a whole. Kugler (1978) found that the morphology of the sting apparatus "does not support the unity of the Myrmecinini," while Wheeler and Wheeler (1954) found for larval characters that "each of the five genera studied might as well be in a different tribe," and later found considerable differences between the larvae of *Acanthomyrmex ferox* and *A. notabilis* (Wheeler and Wheeler, 1977, 1983, and in preparation).

However, *Pristomyrmex* and *Myrmecina* show a number of apparent synapo-

TABLE 1. EXTENDED.

Character																								
19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
?	0	?	0	?	?	0	?	0	?	?	?	?	?	?	0	?	?	?	?	0	0	?	?	?	?
?	1	1	1	0	0	0	?	0	0	0	1	1	?	?	0	1	1	1	0	1	1	0	?	?	?
0	1	1	1	0–1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1	0	0	1	0
0	P	1	1	1	0	0	1	0	1–2	1	0	0	1	0	0	1	1	0	0	1	1	1	0	1	0
1	?	0	0	?	1	?	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	1	?	1	?
1	1	1	1	2	P	0	1	1	2	1	0	0	0	1	0	0	1	1	P	0	1	1	P	1	0
?	1	1	1	2	0	0	?	1	2	0	0	0	0	1	0	0	1	1	1	0	1	P	1	?	0
?	1	1	1	1	0	1	1	0	0–1	P	1	1	0	0	0	1	1	1	0	0	1	1	P	1	0
?	0	0	P	1	0	0	?	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	?	0
?	0	0	1	0	1	1	?	0	?	1	1	1	1	0	0	1	0	0	1	0	0	1	0	?	1
0	?	0	0	?	1	?	0	0	0–1	0	1	1	1	0	0	1	0	0	1	0	0	1	?	1	?
1	0	0	0	0	0	P	0	0	0	P	0	0	P	0	0	1	P	0	1	P	0	1	0	P	P
0	1	1	P	1	P	1	0	0	0–1	0	0	0	1	0	1	1	0	0	1	1	P	1	0	0	0

morphies with *Acanthomyrmex*, including the shortened, stocky trunk in workers; the obsolete promesonotal suture; and the narrow flange encircling the base of the shaft of the scape above the basal condyle (found in some other myrmicines, but particularly well-developed here, especially in *Acanthomyrmex* and *Pristomyrmex*). In addition, workers of most *Pristomyrmex* species have pronotal spines, and many have densely foveate sculpturing on their heads and trunks remarkably similar to *Acanthomyrmex* species; these characters may represent synapomorphies.

An alternative is that *Acanthomyrmex* is not in the Myrmecinini, but rather is close to *Pheidole*. Strong suggestive evidence can be found in the recent description of an unusual myrmicine species from the Miocene or late Oligocene taken from amber from the Dominican Republic (Wilson, 1985). The species *tethepa* is placed in *Pheidole* by Wilson, and is evidently either closely allied to or in that genus. The similarity in cephalic characters can be readily appreciated by comparing Wilson's Figure 4 to the head of *Acanthomyrmex* minors such as *A. nota-*

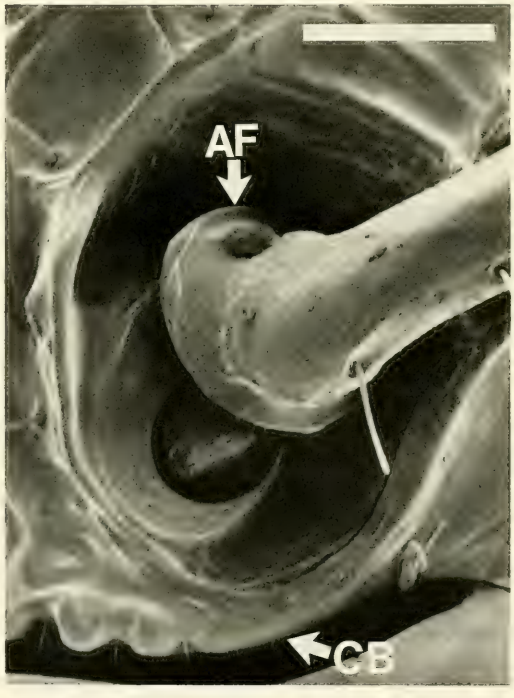


Figure 1. Antennal base and lateral clypeal border in *Acanthomyrmex ferox*. AF = basal flange on antenna; CB = clypeal border.

Scale line. 0.10 mm.

bilis (Fig. 57). The strongly bulging eyes, the massive mandibles, and the small, well-separated mandibular teeth are possible synapomorphies. That *tethepa* is not a species of *Acanthomyrmex* is evidenced by a number of conspicuous characters, such as the elongate trunk, which has a very conspicuously impressed promesonotal suture, and the lack of a medial clypeal hair. Unfortunately, the major worker caste of this species is not known.

Character Polarity

Although relationships among the outgroups are unclear, character states could be assigned for the ancestral conditions of *Acanthomyrmex* on the assumption that *Pristomyrmex* and *Myrmecina* are the two genera most closely related to *Acanthomyrmex*. If the state of a character was consistent within and between both these groups, the ancestral condition for *Acanthomyrmex* could unambiguously be assigned that state. If there was some variation in states, however, more distantly related genera had to be considered. For this purpose all of the additional genera which Emery (1922) placed in the tribe Myrmecinini were treated as possibilities. When the state for that character did not vary within or between any of these genera (based on material available at the Museum of Comparative Zoology at Harvard), that state was assigned as the ancestral condition for *Acanthomyrmex* (unless either *Pristomyrmex* or *Myrmecina* showed the opposite state to that occurring in more distantly related groups, and it was impossible to assign a character state to the other of these two genera). For all other characters the ancestral state was given as uncertain.

This procedure is conservative in that before any ancestral state can be assigned as the ancestral condition of *Acanthomyrmex*, that ancestral condition must be supported by all possible outgroup trees. My assumptions are that *Myrmecina* and *Pristomyrmex* are the two groups most closely related to *Acanthomyrmex* and do not in themselves form a clade, and that one or more of the other myrmecinine genera represent the next closest outgroups.

In a separate, very preliminary analysis, I discarded the hypothetical myrmecinine ancestral species and used the single species *Pheidole tethepa* as the outgroup for the genus *Acanthomyrmex*. Further studies on the phylogeny of *Pheidole* and allied genera will be required to evaluate whether *Acanthomyrmex* is in fact more closely related to *Pheidole* than *Pristomyrmex*, and, if so, to make possible a better resolved hypothetical outgroup for studies of *Acanthomyrmex* phylogeny.

Cladistic Analysis

The entire data set was analyzed using the branch-and-bound method option of Swofford's PAUP program, which is based largely on the ideas of Hendy and Penny (1982). This method is guaranteed to find the shortest trees.

Results

One of the five most parsimonious trees produced when a myrmecinine outgroup is used is given in Figure 2. The other, equally parsimonious trees differ from the first in having either *Acanthomyrmex dusun* or *A. careoscrobis* as the sister taxon to the remaining *Acanthomyrmex* species, or having *A. dusun* at the base of the *notabilis* species group clade, or *A. careoscrobis* at the base of the *luciolae* species group clade. Uncertainties in the placement of *A. dusun* and *A. careoscrobis* probably will be resolved upon collection of the minor worker caste of the former species, and the major worker caste of the latter.

These results suggest the possibility that both the *notabilis* and *luciolae* species groups are monophyletic (as in Fig. 2). The most significant character distinguishing these groups is the conspicuously emarginate posterior margin of the heads of major workers in species of the *luciolae* group (including *A. dusun*), versus the

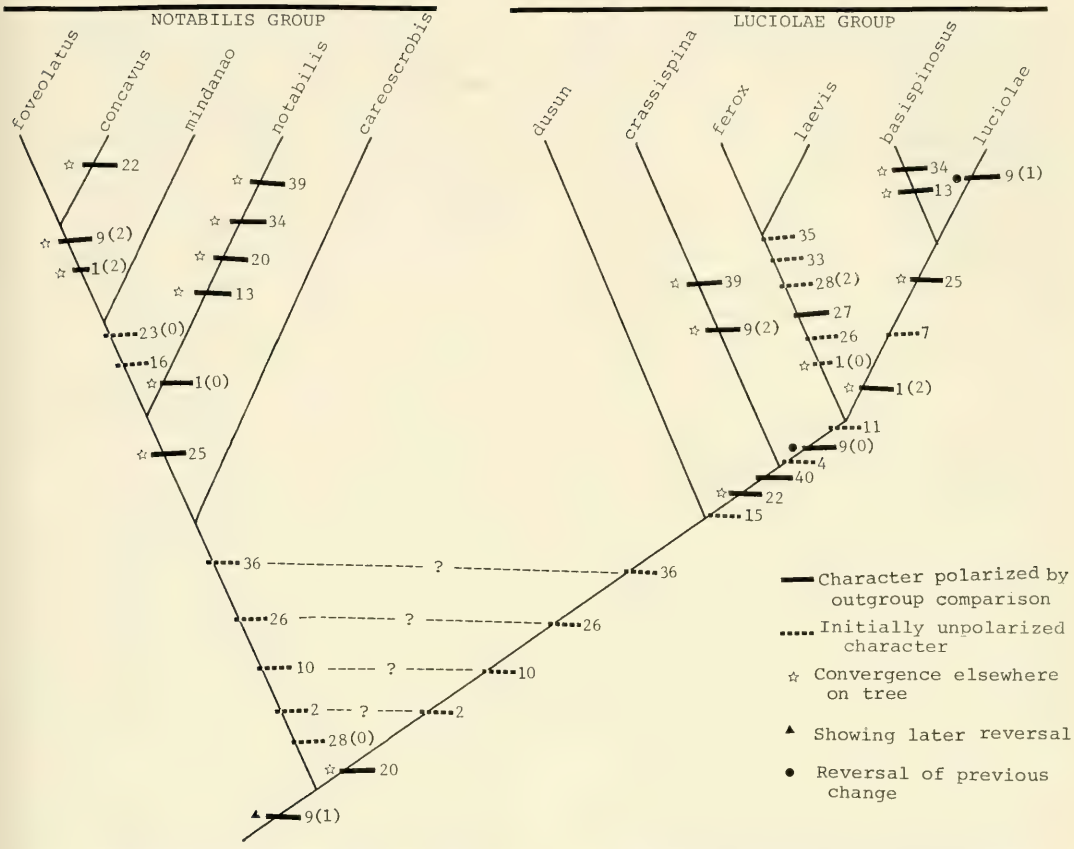


Figure 2. Proposed phylogeny of the genus *Acanthomyrmex*, given a hypothetical myrmecinine outgroup. Four additional, equally parsimonious trees differ only in the position of the species *dusun* and *careoscrobis*, as discussed in the text. All character state changes for initially polarized characters are mapped, but for simplicity only those unpolarized characters which show no homeoplasy within the *Acanthomyrmex* tree are shown. Numbers refer to characters as described in Table 1. Derived states are indicated in parentheses for multistate characters. Tree length: 78 steps.

more evenly rounded margin characteristic of majors in *notabilis* group species. The placement of the species in which the major caste has not yet been described (particularly *careoscrobis* and *concavus*) should be considered tentative.

Two trees are most parsimonious when *Pheidole tethepa* is used as the outgroup. The first is identical to the tree shown in Figure 2, except it is rooted just below *ferox* and *laevis*, such that the *ferox-laevis* clade is the sister to all other *Acanthomyrmex*. Thus now the *luciolae* species group is paraphyletic, with *A. dusun* representing the sister species to the *notabilis* group. The other tree is similar, but the species *crassispinosa* is displaced so as to represent the sister group of all other *Acanthomyrmex*. In addition the *ferox-laevis* and *basispinosus-luciolae* clades now form a monophyletic group. Given that *Acanthomyrmex* is related to *Pheidole*, both of these phylogenies would appear to be reasonable, since the emarginate head characteristic of *Pheidole* major workers is treated as the ancestral condition for *Acanthomyrmex*.

TERMINOLOGY AND CHARACTER STATES

All available *Acanthomyrmex* material was examined in detail for differences in

morphology before any attempt was made to distinguish species. The range of variation in those traits which showed appreciable differences between series was then apportioned into two or more discrete character states, regardless of whether the trait varied continuously or in a discrete manner. The resulting character state codes were then used in delineating species and for phylogenetic analysis.

The characters used in this revision are defined below (excluding characters for which one of two character states is unique to one species), along with the coding for each character state. Definitions of several commonly used terms are also given here. Sculpturing terminology follows that of Harris (1979). Measurements were made with an ocular micrometer on a Leitz microscope; all are significant to at least 0.01 mm. Indexes such as CI were calculated before converting micrometer units to millimeters. Scanning electron micrographs were prepared with a AMR 1000a SEM, using uncoated or gold-palladium coated specimens.

When not otherwise indicated, descriptions apply to both minors and majors.

Characters on Head Capsule (Excluding Clypeus)

Cephalic hollow (major workers). **Character states**: large, medial depression in vertex of head [0] either shallow and ill-defined or absent; or [1] prominent.

CI (Cephalic index). 100 × HW/HL. **Character 1, states** (minor workers): [0] at most 110; [1] intermediate; or [2] > 120. **Character 2, states** (major workers): [0] at most 95; or [1] > 95.

Darkly pigmented streak (major workers). Medial black line on head visible in dorsal full-face view [0] absent; [1] very short, only at back margin of head; or [2] longer, extending farther rostrad onto dorsal surface of head.

EL (Eye length). Diameter of eye in full-face view.

Frontal sulcus. **Character 1, states**: [0] minor workers without a short, wide sulcus conspicuous immediately above frontal area; or [1] sulcus present. **Character 2, states**: [0] major workers without a wide, deeply impressed sulcus between cephalic hollow and frontal area; or [1] sulcus present.

Full face. Head viewed dorsally so as to attain the maximum length.

Greatest head width. **Character states**: maximum HW is [0] about equal above and below eyes (difference 2% or less); or [1] greatest above the eyes.

Head shape (minor workers). **Character states**: in dorsal full-face view, back margin of head [0] rounded except for a very shallow medial concavity (e.g., Fig. 57); [1] moderately concave all the way across (Fig. 15); or [2] deeply concave, so that the posterior corners of the head are produced back into prominent, lateral lobes (Figs. 9, 44).

Head shape (major workers). **Character states**: in full-face view, back margin of head [0] distinctly bilobed (Fig. 11); or [1] evenly rounded, at most slightly emarginate medially (Fig. 48, 59).

HL (Head length). The maximum distance from the base of the medial hair on the clypeus to the medial point on the posterior margin of the head.

HW (Head width). The maximum width across the head in full-face view, excluding the eyes.

Hypostomal teeth (major workers; invariably present in minors). Small rounded projections, one located laterally near base of each mandible. **Character states**: teeth [0] absent; or [1] present.

Pilosity density. **Character states**: long erect to suberect hairs on head [0] numerous; or [1] very scattered.

Pilosity height. **Character states**: longest of the hairs on dorsum of head extending [0] < 0.10 mm; or [1] > 0.12 mm.

Sculpture (cephalic) (minor workers). **Character states**: dorsal and lateral surfaces of head capsule with [0]

rounded (or ellipsoidal) foveae having thick, curving walls; or [1] at least those foveae on vertex and adjacent to scrobes with angular borders, and separated by thin, lamellar walls.

Sculpture (cephalic) (major workers). **Character 1, states**: foveae [0] relatively small; or [1] large. **Character 2, states**: frons [0] lacking costate sculpture; or [1] sculpture present.

CHARACTERS ON CLYPEUS, MANDIBLES AND ANTENNAE

Clypeal index. The shape of the region of the clypeus between the frontal carina was measured as 100 × W/H where "W" is the minimum distance between the raised edges of the frontal carina, and "H" is the distance from the posteriormost point on the frontal area to the base of the medial clypeal hair. **Character states**: [0] at most 125; or [1] > 125.

Clypeal rugae (minor workers). Two longitudinal rugae extend through the clypeus from near the bases of the lateral clypeal hairs, delineating a medial clypeal region between them (e.g., Fig. 15). **Character states**: these rugae are [0] absent or incomplete; or [1] well-developed.

Funicular index. An index of funicular thickness: maximum width of funicular segments II and III (which are similar in shape) divided by the average length of the same segments (half the combined lengths of the segments). **Character states**: funiculi [0] thick, with index > 1.20 (or > 1.50 in majors); or [1] thinner.

Lateral hair on clypeus (minor workers). Long hair projecting forward at either side of medial hair from anterior margin of clypeus (Fig. 3). **Character states**: base of each lateral clypeal hair [0] not completely enclosed by a low wall; or [2] hair in a well-developed oval fovea (Fig. 3).

Medial hair on clypeus (minor workers). Hair projecting forward from anterior margin of clypeus medially (Fig. 3).

Medial clypeal lobes (minor workers). A small, narrow projecting lobe located immediately to either side of medial clypeal hair, and mesad to the lateral clypeal hair (Fig. 3). **Character states**: lobes [0] feebly developed; or [1] strongly projecting.

Medial projection (major workers). **Character states**: [0] anterior margin of clypeus without a projecting medial lobe, although often with low, feebly rounded lobes (e.g., Fig. 17); or [1] projection present (Fig. 25).

MI (Mandible index). 100 × ML/HL.

ML (Mandible length). Distance between basal condyle and apical tooth of mandible.

SI (Scape index) (minor workers; little variation in majors). 100 × SL/HW. **Character states**: [0] at most 90; or [1] > 90.

SL (Scape length). The maximum length of the scape (excluding the wide flange at its base and the basal radicle beneath it).

Ventral mandibular tooth (minor workers). A tiny inward-projecting denticle present along the medioventral border of each mandible, where, in majors, a massive blunt projection is invariably present. **Character states**: denticle [0] absent, or [1] present.

CHARACTERS ON TRUNK AND LEGS

Femur concavity. **Character states**: ventral surface of each femur [0] convex or somewhat flattened; or [1] with a well-developed concave groove (at least in hind femora).

Femur pilosity. **Character states**: [0] each femur with at most two erect to suberect hairs visible in profile (in which case hairs typically present proximad on ventral face of shaft); or [1] hairier.

FLI (Femur length index). 100 × HFL/HL. **Character states**: index [0] at most

120 (or at most 60 in majors); or [1] greater.

FWI (Femur width index). 100 × HFW/HFL, where HFW is the maximum width of the hind femur in lateral view. **Character states**: [0] index at most 18; or [1] greater.

HFL (Hind femur length). Maximum length of the hind femur.

Pronotal angle. **Character states**: [0] anterior ventrolateral margin of pronotum curved to sharply angled, but without a small but distinct tooth (e.g., Fig. 16); or [1] tooth present (Fig. 24).

Pronotal spine length (minor workers). **Character states**: [0] pronotal spines short and stubby, conspicuously shorter than propodeal spines (Fig. 52); [1] pronotal spines long, but not longer than propodeal spines; or [2] pronotal spines longer than propodeal spines (Fig. 24).

Pronotal spine pilosity. **Character states**: pronotal spines each with [0] at most two prominent erect to suberect hairs visible in profile; or [1] hairy (with more than two hairs).

Propodeal declivity. **Character states**: declivity of propodeum with [0] at most a single distinct rugum bordering each side, extending from the base of the propodeal spine; or [1] with two adjacent rugae along each border.

Propodeal spine length. Measured from the tip of the spine to the closest border of the propodeal spiracle. **Character states**: [0] propodeal spine less than half as long as length of head (HL) (or less than 25% of HL in majors); or [1] longer.

Propodeal spiracle diameter (major worker; little variation in minors). **Character states**: [0] diameter of spiracle less than 2% of HL; or [1] spiracle opening larger.

Characters on Petiole, Postpetiole, and Gaster

Anterior peduncle length, petiole. **Character states**: anterior peduncle relatively short and deep (e.g., Fig. 43); or [1] peduncle long and more slender (e.g., Fig. 47).

Gaster pilosity. **Character states**: [0] gaster with numerous erect or suberect hairs (usually densest dorsad); or [1] gaster with very few hairs or bare.

Lateral petiolar hairs. **Character states**: [0] an erect hair extends laterally from each side of anterior petiolar node just caudad of the spiracle; or [1] hair lacking.

Petiolar index. 100 × PL/PH, where PL is the distance from the posterior margin of the petiolar spiracle to the dorsalmost point on the posterior margin of the posterior peduncle, with the petiole viewed in profile; while PH is the height of the posterior peduncle of the petiole. **Character states**: index [0] < 170; or [1] > 180.

Petiolar spines. **Character states**: petiolar node [0] lacking long spines laterally at apex although often with short lateral denticles (Fig. 8A–C); or [1] long spines present (Fig. 8D–F).

Postpetiole narrowness. **Character states**: [0] node relatively long, greater than 60% as long as it is wide in dorsal view; or [1] narrower.

Postpetiole node. **Character states**: [0] node high and rounded, sculpture lacking or foveate; or [1] node low, slightly convex or flattened, and rugose.

Postpetiole pilosity. **Character states**: dorsal face of postpetiole with [0] two pairs of hairs; or [1] pilosity different.

PWI (Petiolar spine width index). In dorsal view, distance between apical spines or denticles relative to the greatest width of petiole basally at node. **Character states**: tips of spines [0] close together (PWI < 65); [1] intermediate (PWI 65 to 100); or [2] projecting laterally (PWI > 100).

Sublateral petiolar hairs. **Character states**: [0] no erect hair extends ventrolaterally from each ventrolateral face of the anterior petiolar node at a posi-

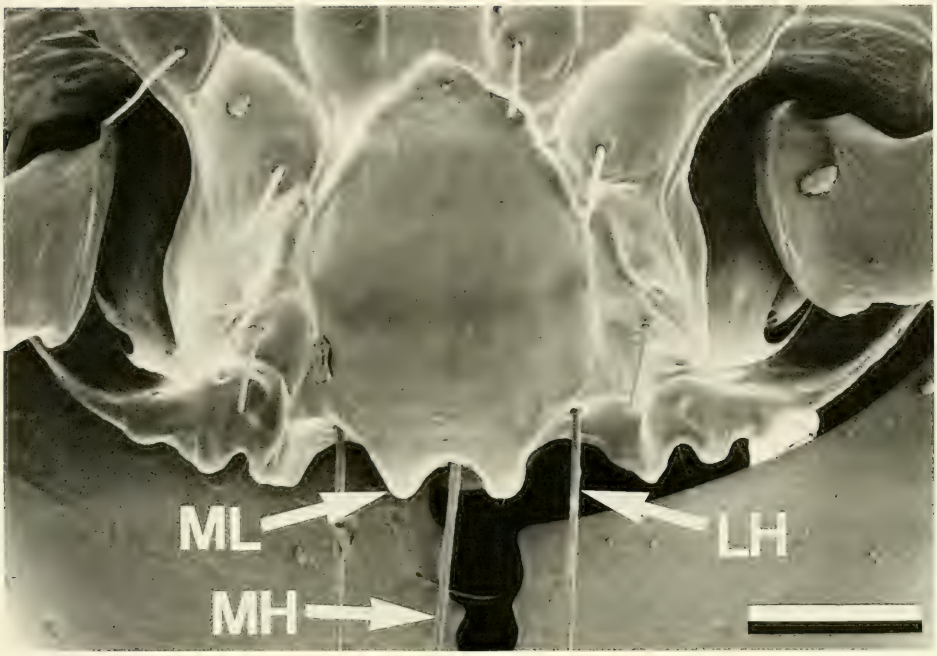


Figure 3. Clypeus of *Acanthomyrmex ferox*. MH = medial clypeal hair; LH = lateral clypeal hair; ML = medial clypeal lobe. *Scale line*. 0.10 mm.

tion more or less below the lateral petiolar hair (when present); or [1] hairs present.

Subpetiolar declivity. **Character states**: ventral margin of petiole [0] lacking a conspicuous sharp declivity in profile (Fig. 14); or [1] with such a declivity located slightly anterior to and below petiolar spiracle (Fig. 28).

LOCALITY DATA AND REFERENCE COLLECTIONS

The collector(s) of each series and the museum(s) in which the material is deposited is given in parentheses following the locality data for each series examined. Names of museums are abbreviated as follows: British Museum (Natural History), London (BMNH); Museo Civico di Storia Naturale, Genoa (MCSN); Museum d'Histoire Naturelle, Geneva (MHN); and Museum of Comparative Zoology, Cambridge (MCZ).

Acanthomyrmex

Acanthomyrmex Emery, 1893: 244. Type species *Acanthomyrmex luciolae*, designated by Emery 1922: 235.

Diagnosis. Dimorphic myrmicine ants. Worker castes with trunks short and stout, convex dorsally in profile except for prominent propodeal spines (and usually with cylindrical humeral spines in minor workers); antennae 12-merous, with scape having a thin, plate-like flange encircling its base. Major caste with head huge, articulating with trunk ventrally so that the vertex of the head projects back over the trunk. Minor workers with a prominent medial hair on anterior border of clypeus.

Minor Worker. Small to moderate sized ants (total length 2.7 to 5.0 mm), usually with little size variation within a series. Head large (ca. 50% wider than trunk), wide (CI at least slightly greater than 100); head width 0.70 to 1.23 mm. Cephalic sculpture typically densely foveate, occa-

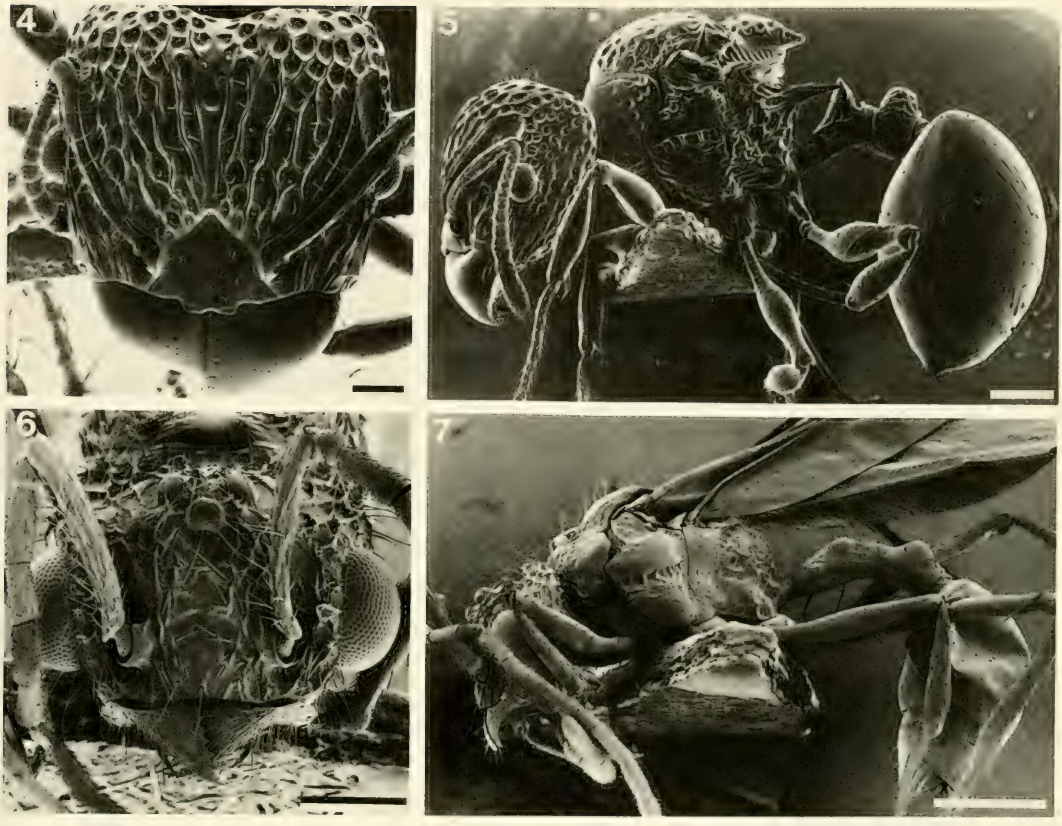
sionally alveolate or virtually smooth. Eyes moderately large (length of eye in full-face view 17 to 25% of head length), oval, and strongly convex; located mediolaterally, with the distance between anterior margin of eye and mandible bases representing 24 to 34% of head length. Antennal fossae far apart, at anterior margin of head. Feeble scrobe usually present dorsad to eyes for all or at least the basal part of the scape (bent downwards apically in some species to accommodate part of the funiculus); the frontal carinae extend back to form the dorsalmost borders of the scrobes. Antennae 12-merous, moderately thick, with a three-segmented funicular club; club about as long as remainder of funiculus excluding basal funicular segment. There is a prominent flange above the basal radical, forming a thin, disk-shaped "base" to the scape.

Clypeus produced back between bases of antennae; posterolateral borders of clypeus raised to form trenchant ridges which border the antennal fossae in front. Clypeus usually with lateral foveae or rugae; anterior margin with several small, well-separated projecting lobes and with a prominent medial hair. Mandibles massive (MI 69 to 92), with a wide, subtriangular blade which curves ventrad toward apex, with the margin having four to ten tiny teeth separated by wide gaps in addition to two relatively prominent apical teeth; dorsal mandibular surfaces feebly punctate and with a very feeble rugulose microsculpture. Maxillary palpi with four segments; labial palps with three (*A. basispinosus* and *mindanao* examined).

Trunk very short and robust, evenly convex in profile, with anterior margin of propodeum not at all impressed dorsally; trunk diminishing in width posteriorly. Pronotum fused with mesonotum; promesonotal suture obsolete. Propodeum invariably bispinose; pronotum generally armed with dorsolateral spines, which are located anterodorsally to the dorsalmost point reached by the groove between the pronotum and mesothorax laterally. Sculpture foveate on pronotum and dorsally on trunk; areolate-rugose on pleura of remainder of trunk, and smooth on declivity of propodeum. Petiole pedunculate in front; node usually with dorsolateral denticles or spines. Postpetiole variable, low and rounded dorsally or with a prominent node; usually rugose. Gaster oval, less wide than head, and longer than deep. Legs moderately long, with hind femora 85 to 148% as long as head; middle and hind tibiae with a single basal spur. Long, erect to suberect pilosity generally dense on head, sparser on trunk, and variable on legs, petiole, postpetiole and gaster; on head hairs mostly arise from foveae.

Major Worker. Head enormous, appearing greater in volume than remainder of body, and of a length about twice that of trunk or longer. Foramen located ventrally far from posterior margin of head, with the portion of the head behind the foramen extending back over the trunk; trunk partially hidden within a cavity beneath head posteriorly. Cephalic sculpture foveate (at least on vertex), but with foveae generally small, shallow and sparse relative to those of minor workers. Ocelli lacking; compound eyes similar to those of minor worker, but slightly more anterior on head, and of a length 9 to 14% of that of the head. Antennae similar in size to those of minor workers, and thus much smaller relative to head size; scrobes as described for minors but more prominent, with a shallow recess for basal portion of funiculus typically also present dorsad to eyes. Clypeus smooth, without small projecting lobes along anterior margin, and usually lacking pilosity. Mandibles massive, similar to minors but smaller relative to head size (MI ca. 50 to 60), typically with dorsal masticatory margin worn; with a ventral process shaped like a massive, blunt tooth beneath mandible basally (occasionally present as small denticle in minors). Trunk, waist, and gaster similar to minors, but pronotal spines lacking, and pronotum smooth anteriorly.

Queen. Previously undescribed. Head



Figures 4–7. Queen and male of *Acanthomyrmex ferox* (from Kalimantan). 4. Frontal view of head, queen. 5. Lateral view, queen. 6. Frontal view of head, male. 7. Lateral view, male.

Scale lines. Figures 4 and 6, 0.25 mm. Figures 5 and 7, 0.50 mm.

(Fig. 4) smaller than in major caste, and attached to trunk nearer to posterior margin of head; not projecting back over trunk. Mandibles, antennae and compound eyes similar to worker castes, and (relative to head length) intermediate in length between those of majors and minors; ocelli present. Clypeus as in majors. Mandibles each with a ventral process like those of majors. Trunk (Fig. 5) very short and stout, quadrate in lateral view; in dorsal view rounded, almost as wide as long. Pronotal spines lacking; propodeal spines present. Scutellum dorsolaterally with short, thick spines projecting posteriorly above propodeal spines; posterior margin of scutellum directly above that of propodeum. Known only for *A. ferox*; for further details see *ferox* description.

Male. Previously undescribed. Head (Fig. 6) broad; eyes similar to those of queen but much larger relative to head size (length about 40% of that of head). Antennal scrobes absent. Antennae 13-merous. Scapes thick, not reaching posterior margin of head, and virtually lacking a basal flange. First and seventh funicular segments very short, about as long as broad, with the segments between them each about a third the length of scape; third and fifth segments somewhat compressed (others cylindrical), the fifth curved; segments beyond the sixth longer, and progressively lengthening distally

(terminal segment about 80% of scape length). Mandibles as long relative to head length as in queen or major, but much less massive, only very slightly curved ventrad apically; the six to eight teeth along masticatory margin less reduced than in female castes, and without large gaps between them; ventral mandibular process lacking.

Trunk (Fig. 7) similar to that of queen, but somewhat longer; mesonotum with an impressed Mayrian furrow; scutellum higher; propodeum lacking spines, pinched laterally below spiracles, and extending out posteriorly beyond back margin of scutellum. Postpetiole with node very low and rounded; postpetiole low, smooth, and more elongate than in females; legs long and slender. Parameres curving sharply ventrad midway along length, with narrow, rounded tips having very short pilosity. Digitus heavily sclerotized, curving strongly ventrad near base, and rounded distally; cuspidal lobes very low and inconspicuous. Aedeagus subrectangular, ventral margin serrate, with tiny, very sharp recurved teeth. Wings as in *Pristomyrmex*, but with a complete discoidal cell (m-cu vein present).

Male known only for *A. ferox*; for further details see description of that species.

Larva. Known for two species. The larvae of *A. ferox* are considerably different from those of *A. notabilis* (see Wheeler and Wheeler, 1977, 1983, and in preparation). The differences are strong enough to suggest separation at the generic or even tribal level (Wheeler and Wheeler, personal communication). The alternative is a rapid evolution of the larvae within the genus *Acanthomyrmex* (see section on relationships).

Synonymic List of Species

luciolae group.

basispinosus sp. nov. Sulawesi.
crassispina Wheeler, 1930. Taiwan.
dusun Wheeler, 1919. Sarawak.
ferox Emery, 1893. Peninsular Malaysia, Borneo, Sumatra.
laevis sp. nov. Peninsular Malaysia.
luciolae Emery, 1893. Sri Lanka.

notabilis group.

careoscrobis sp. nov. Sarawak.
concavus sp. nov. Sarawak.
foveolatus sp. nov. Sarawak.
mindanao sp. nov. Philippines, Sarawak.
notabilis (Smith), 1860. Moluccas, Sulawesi, Seram.

Misplaced *Acanthomyrmex*

Acanthomyrmex kochi Emery, 1909: 252, fig. 1. Minor worker from Etna Bay, New Guinea. The complete promesonotal suture, deeply impressed metanotal groove, finely punctate cephalic sculpture and other characters are at variance with all other material ascribed to *Acanthomyrmex* (Emery, 1922). This appears to be a *Pheidole* (*Pheidolacanthinus*).

Key to *Acanthomyrmex* Minor Workers

The minor workers of *A. dusun* and *foveolatus* are unknown.

1. Head convex across posterior margin, with at most a feeble medial concavity in full-face view (Fig. 57) 2
– Head distinctly concave across posterior margin 4
2(1). Petiole without long, cylindrical spines laterally on apex of node (Fig. 62) ..... *notabilis*
– Such spines are present (Fig. 8D–F) 3
3(2). Head with conspicuous alveolate sculpture ..... *ferox*
– Head virtually free of sculpture, smooth ..... *laevis*
4(1). Head deeply concave across posterior margin (Figs. 9, 44) 5
– Head feebly concave across posterior margin in full face view (e.g., Fig. 15) 7
5(4). Propodeal spines in profile with a wide basal portion abruptly narrowing to shaft of spine (Fig. 10) ..... *basispinosus*
– Propodeal spines lack a distinct wide base 6
6(5). Gaster with numerous long erect to suberect hairs; from Sri Lanka ..... *luciolae*
– Gaster virtually bare; from Sarawak ..... *concavus*
7(4). Propodeal spines somewhat laterally compressed, appearing blade-like in lateral view (Fig. 16); from Taiwan (Lanyu Island) ..... *crassispina*
– Propodeal spines, cylindrical, not at all blade-like 8
8(7). Well-developed small projecting lobes immediately on each side of medial hair

on anterior margin of clypeus; funicular scrobes present ..... *mindanao*
– Medial clypeal lobes poorly developed; scrobes for scapes present, but these not bent down posteriorly to form funicular scrobes above eyes ..... *careoscrobis*

KEY TO *ACANTHOMYRMEX* MAJOR WORKERS

The major workers of *A. careoscrobis*, *concavus*, and *laevis* are unknown.

1. Posterior margin of head conspicuously bilobed when head viewed in full-face (*luciolae* group, e.g., Fig. 11) 2
– Posterior margin of head not strongly bilobed, at most slightly emarginate mesad (*notabilis* group, e.g., Fig. 48, 59) 6
2(1). Propodeal spines somewhat laterally compressed, appearing blade-like in lateral view (Fig. 18); from Taiwan (Lanyu Island) ..... *crassispina*
– Propodeal spines, cylindrical, not at all blade-like 3
3(2). Propodeal spines in profile with a wide basal portion abruptly narrowing to shaft of spine (Fig. 12) ..... *basispinosus*
– Propodeal spines lack a distinct wide base 4
4(3). Node of petiole with long lateral spines at apex (Fig. 8D–F)[2] ..... *ferox*
– Without long spines on petiole 5
5(4). Head costate across frons; from Sri Lanka ..... *luciolae*
– Head lacking costae; from Borneo ..... *dusun*
6(1). Postpetiole wide, less than 60% as long as it is wide in dorsal view ..... *notabilis*
– Postpetiole about as wide as it is long in dorsal view 7
7(6). Dorsum of head with tiny, shallow foveae except for large foveae bordering antennal scrobes (Fig. 48) ..... *foveolatus*
– Foveae larger (Fig. 53) ..... *mindanao*

THE *LUCIOLAE* GROUP

Posterior margin of head in major workers emarginate, so that the back of the head is distinctly bilobed in full face view. Other characters: propodeal spiracle opening in majors larger and more conspicuous than in *notabilis* group majors; basal funicular segments in both castes tending to be relatively slender (width of the second and third funicular segments less than 25% greater than their average length in minor workers, and less than 50% in majors); hypostomal teeth invariably present in majors. Except in *A. crassispina*, dorsal surface of gaster with numerous scattered hairs.

Species in this group are known from Sri Lanka, Peninsular Malaysia, the Malay Archipelago, and Taiwan.

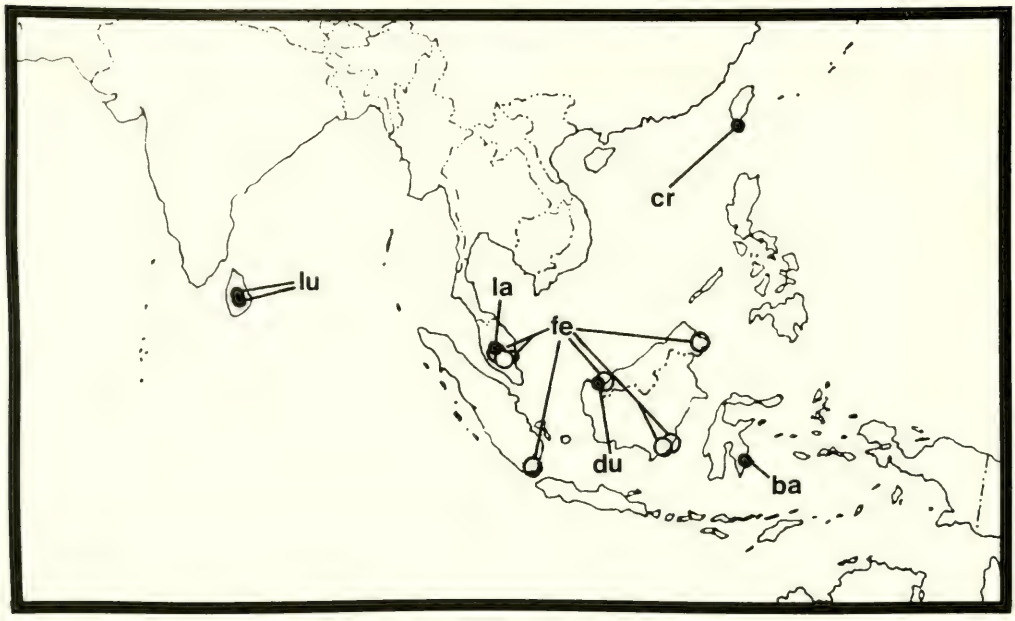
Acanthomyrmex basispinosus new species
Figures 8A, 9–14; Map 1

Holotype. Minor worker deposited in MCZ from Indonesia: S.E. Sulawesi: 1–2 km east of Wolasi, 42 km south of Kendari, ca. 350 m, rotten wood in rainforest, W-46, 13–14 July 1972 (W. L. Brown, Jr. [examined]). Name derived from Latin *basis* + *spina*, referring to the widened bases of the propodeal spines.

Diagnosis. Propodeal spines of both castes with distinctive widened bases (Figs. 10, 12; postpetiole narrow, much wider than long in dorsal view.

Minor. Holotype (HW 1.08) and five minor worker paratypes measure HW 0.98 to 1.13, HL 0.95 to 1.08 (CI 103 to 105), ML 0.18 to 0.19 (MI 72 to 77), SL 1.06 to 1.20 (SI 97 to 115), EL 0.21 to 0.23, HFL 1.28 to 1.39 (FLI 124 to 136; FWI 16 to 17) mm. Head strongly concave across posterior margin in full-face view, and thus similar in shape to *A. luciolae* and *concavus*, except less broad (CI < 120), and lateral margins relatively more convex; widest above eyes. Head with rounded, thick-walled foveae (although foveae near scrobe, on side of head and on vertex with thinner walls, and thus approach the condition described for *A. ferox*). Dorsum of head with longest hairs extending about 0.18 mm. As in *A. notabilis*, short but conspicuous wide sulcus present mesad between the eyes above the frontal area (traces of such a sulcus present in some *A. luciolae*, *crassispina* and *concavus* specimens). Clypeal index 102 to 110. Lobe to each side of medial clypeal hair moderately to strongly produced; lateral clypeal

[2] Presumably the major of *A. laevis* will also key out here.



Map 1. Distribution of the species in the *luciolae* species group.

Abbreviations: ba = *A. basispinosus*, cr = *A. crassispinosa*, du = *A. dusun*, fe = *A. ferox*, la = *A. laevis*, lu = *A. luciolae*.

hairs in a completely enclosed fovea. Rugum extending back across clypeus from each of these medial clypeal lobes present, though poorly developed. Mandibles lacking a ventral tooth.

Spines on trunk virtually straight. Propodeal spines somewhat longer than those on pronotum; in the two largest specimens (HW for both 1.13 mm) propodeal spines considerably longer, as pronotal spines are very short and stubby. Propodeal spines with a distinctive widened base in profile. Pronotal spines without conspicuous hairs. Pronotal angle abrupt but not forming a feeble tooth. Propodeal declivity bordered on each side by two adjacent rugae, which extend down from base of each propodeal spine (second rugum feeble).

Node of petiole as in Figure 8A, without sharp lateral denticles; PWI intermediate (79 to 84). Anterior peduncle of petiole long and narrow, with the lateral hairs present and sublateral hairs lacking; subpetiolar declivity absent. Postpetiole nar-

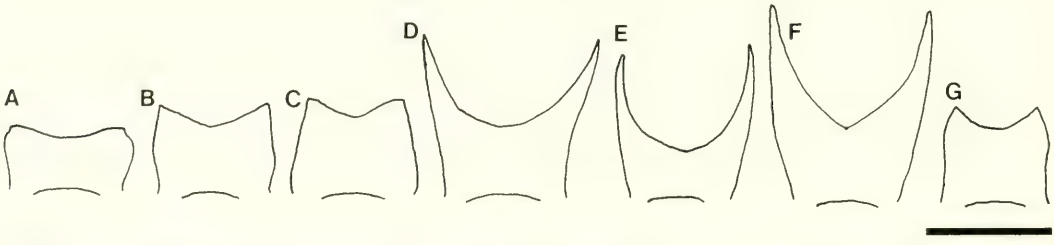


Figure 8. Petiolar nodes of minor workers in posterior view: *luciolae* species group. A. *A. basispinosus* paratype; B. *A. crassispina* syntype; C. *A. dusun* holotype (major worker); D. *A. ferox* syntype; E. *A. ferox* (*A. dyak* syntype); F. *A. laevis* paratype; G. *A. luciolae* syntype.

Scale line. 0.25 mm.

row, almost twice as wide as it is long in dorsal view, and with a high, narrow node; thus the postpetiole resembles that of *A. notabilis*. Femora with scattered hairs, and conspicuously concave beneath; hind femora relatively slender (FWI < 18). Color orange yellow or reddish yellow, legs lighter yellow.

Major. The two paratypes measure HW 2.10 to 2.18, HL 2.17 to 2.24 (CI 97), SL 1.18 (SI 54 to 56), EL 0.28, HFL 1.40 to 1.44 (FLI 64; FWI 16) mm. Foveae on head denser, more deeply impressed, and somewhat larger than in *A. crassispina* and *dusun*. Without a distinct cephalic hollow. Long feeble darkly pigmented medial streak dorsad on head; wide medial sulcus conspicuous on frons. Clypeal index larger than in minors: 126 and 139. Forward margin of clypeus lacking a medial projection (but with two feeble, rounded lobes medially). Propodeal spines as described for minor worker.

Paratypes. Two majors and five minors, same date and collection number as holotype (MCZ, BMNH).

Additional Records. Known only from type series.

Acanthomyrmex crassispina
Figures 8B, 15–20; Map 1

Acanthomyrmex crassispina Wheeler, 1930: 101–103, fig. 2. Taiwan: Botel Tobago (=Lanyu Island), 6/1926, no. 49, three minor workers (R. Takahashi, MCZ and U.S. National Museum [examined]).

Diagnosis. Both castes with each scape having a small lateral flange proximad; propodeal spines wide and blade-like in profile; pilosity very sparse; from Taiwan.

Minor. Syntypes measuring HW 1.07 to 1.09, HL 0.87 to 0.90 (CI 121 to 123), ML 0.75 to 0.78 (MI 86 to 89), SL 0.97 to 0.98 (SI 90 to 91), EL 0.16 to 0.17, HFL 1.08 to 1.10 (FLI 122 to 125; FWI 23 to 24) mm. Head concave across posterior margin in full-face view, although not as strongly as in *luciolae*. Head widest above eyes. Head with rounded, thick-walled foveae, and dorsally with very few, scattered hairs (these standing 0.08 to 0.10 mm). Scapes virtually smooth, not feebly rugose as in most *Acanthomyrmex*. Scapes also with a distinctive lateral flange extending longitudinally at their bases (Fig. 15). Clypeal index 128–131. Lobe to each side of medial clypeal hair very feeble, and relatively widely separated from the hair; lateral clypeal hairs not in a completely enclosed fovea. A well-developed rugum extends back from each of the medial clypeal lobes, separating a smooth medial clypeal region from the more lateral areas. Mandibles lacking a ventral tooth.

Spines on trunk slightly curved caudad; propodeal spines somewhat longer than those on pronotum, and also slightly compressed laterally so as to appear wide and blade-like in profile. Pronotal spines lacking conspicuous hairs. Pronotal angle not forming a feeble tooth. Sculpture on trunk (particularly on dorsum) relatively feebly impressed. Propodeal declivity bordered on each side by a single rugum extending from the base of each propodeal spine.

Node of petiole as in Figure 8B, PWI intermediate (88 to 92); node lacking the single pair of hairs found low on caudal face of petiolar node of other *Acanthomyrmex* species. Anterior peduncle of petiole relatively short and deep, lacking lateral and sublateral hairs; subpetiolar declivity present. Postpetiole subrectangular, almost as long as it is wide in dorsal view, and with two or three conspicuous rugae on each side; lacking pilosity. Gaster virtually without pilosity. Femora lacking all but basal hairs, and with ventral surfaces flattened or only very feebly concave. Head and trunk orange yellow, with legs yellow.

Major. Individual from Botel Tobago (Lanyu Island, Taiwan) measures HW 1.99, HL 2.11 (CI 94), SL 1.03 (SI 52), EL 0.25, HFL 1.32 (FLI 62; FWI 19) mm. As in the minor, head, trunk, and gaster with very little long pilosity. Head as wide below eyes near mandible bases as above eyes (greatest HW is above eyes in other

species). Shallow oval foveae scattered over head surface, not as dense as in other *luciolae* group species; foveae most numerous laterally and on vertex. Cephalic hollow well-developed, with medial sulcus extending below it to the frontal area shallow and inconspicuous. Darkly pigmented medial streak very short, present between lobes on vertex but not extending to cephalic hollow. Forward margin of clypeus lacking a medial projection, although two low, rounded lobes are present. Propodeal spines moderately long, curved caudad; compressed as in the minor worker. Scape with lateral flange near base. PWI value 100.

Additional Records. TAIWAN: Botel Tobago (=Lanyu Island), three minor workers and one major (T. Kano, MCZ, BMNH). This series lighter yellow in color (except gaster dark brownish yellow); femora convex ventrad.

Acanthomyrmex dusun
Figures 8C, 21–22; Map 1

Acanthomyrmex dusun, Wheeler, 1919: 89. Malaysia: W. Sarawak: Mount Matang, i/1914 (G. E. Bryant, MCZ [examined]).

Diagnosis. Major with head lacking rugae; clypeus with medial projection; propodeal spines short, cylindrical, curved ventrad. Minor worker unknown.

Major. HW 2.00, HL 1.99 (CI 100), SL 0.95 (SI 48), EL 0.21, HFL 1.08 (FLI 54; FWI 21) mm. Shallow oval foveae scattered, somewhat larger and denser near scrobes; traces of longitudinal rugae near scrobes. With a more clearly demarcated funicular scrobe than in any other *Acanthomyrmex* major examined. Cephalic hollow well-developed, with a conspicuous medial sulcus extending below it to the frontal area. Darkly pigmented medial streak on head long, extending into hollow. Clypeal index 178. Forward margin of clypeus with a medial projection. Condition of hypostomal teeth unknown.

Propodeal spines short, conspicuously curved caudad. Pronotal angle drawn out into a feeble tooth. Node of petiole as in Figure 8C, PWI intermediate (ca. 69). Anterior peduncle of petiole relatively short and deep, and with lateral hairs present, but sublateral pair lacking; subpetiolar declivity present. Postpetiole subrectangular, similar to that of *A. crassispina*. Dorsal surface of postpetiole and gaster hairy. Femora hairy, and with ventral surfaces distinctly concave. Color orange yellow.

Additional Records. Known only from holotype.

Acanthomyrmex ferox
Figures 3–7, 8D–E, 23–28; Map 1

Acanthomyrmex ferox Emery, 1893: 245–246, pl. 6, fig. 11. Peninsular Malaysia: Perak, two minor workers (M. M. Staudinger, MCSN and MHN [examined]).

Acanthomyrmex dyak Wheeler, 1919: 86–89. Malaysia: Sarawak: Kuching, two minor workers and one major (J. Hewitt, MCZ [examined]). NEW SYNONYMY.

Diagnosis. Petiolar node of both worker castes with long, dorsally directed lateral spines, and postpetiole with a high, rounded node. Minor worker with conspicuous alveolate sculpture.

Minor. The two syntypes measure HW 1.06 to 1.12, HL 1.00 to 1.05 (CI 106 to 107), ML 0.83 (MI 83), SL 1.26 to 1.28 (SI 114 to 120), EL 0.20 to 0.21, HFL 1.38 to 1.39 (FLI 132 to 139; FWI 19 to 20) mm. Head shape as in *A. notabilis*, i.e., virtually rounded across posterior margin in full-face view, although slightly flattened or with a trace of a concavity mesad. Maximum head width virtually the same above and below eyes. Cephalic sculpture

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Figures 9–14. *Acanthomyrmex basispinosus* paratypes. 9. Frontal view of head, minor worker. 10. Lateral view of trunk, minor worker (insert: lateral view of individual with short pronotal spines). 11. Frontal view of head, major worker. 12. Lateral view of trunk, major worker. 13. Dorsal view of postpetiole, minor worker. 14. Lateral view of waist, minor worker.

Scale lines. Figures 9–12, 0.50 mm. Figures 13–14, 0.10 mm.

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best described as areolate or alveolate rather than foveate, as the foveae have angular walls and are separated by thin partitions; longer hairs on dorsum of head extend 0.15 mm. Clypeal index 91 to 93. Feeble lobe present on each side of medial clypeal hair; lateral clypeal hairs not in a well-defined fovea. Clypeus virtually smooth, and without two longitudinal rugae present to demarcate a medial clypeal region. Mandibles lacking a ventral tooth.

Spines on trunk virtually straight (propodeal spines with a slight curvature caudad); pronotal spines hairy, and consistently longer than those on propodeum. Pronotal angle drawn out into a feeble tooth (Fig. 24: indistinct or absent in some other specimens and on one side of a syntype). Propodeal declivity bordered on each side by a single rugum, as described for *A. crassispina*.

Node of petiole as in Figure 8D–E, PWI wide (120 and 138). Anterior peduncle of petiole relatively short and deep, and with lateral and sublateral hairs; subpetiolar declivity present. Postpetiole smooth (although with feeble foveae on node); with convex lateral margins in dorsal view (rather than rectangular), and almost as long as it is wide. Postpetiole having a distinctive high, rounded node with scattered hairs. Dorsal surface of gaster hairy, but with hair density sparser than in most other *luciolae* group species. Femora hairy, and with ventral surfaces only feebly concave. Orange yellow, with legs and gaster lighter and with more yellow.

Major. Three Sarawak majors from two series (single major from Peninsular Malaysia very similar): HW 2.42 to 2.58, HL 2.45 to 2.48 (CI 99 to 104), SL 1.20 to 1.25 (SI 47 to 52), EL 0.26 to 0.28, HFL 1.54 to 1.56 (FLI 63 to 68; FWI 20) mm. Frons costate up to level of scrobes (and laterally up to level of eyes); vertex relatively densely foveate (comparison of specimens suggests the foveae become denser and more deeply impressed in progressively smaller majors; note that the major in Fig. 25 is relatively large). No distinct cephalic hollow. No darkly pigmented streak dorsad on head; wide medial sulcus conspicuous, low on face. Forward margin of clypeus with a medial projection. Propodeal spines long, as in minors but thicker at bases. Pronotal angle lacking the feeble tooth characteristic of the minor caste.

Queen. Previously underscribed. Three queens (from Peninsular Malaysia, Sarawak, and Kalimantan) measure HW 1.86 to 2.30, HL 1.54 to 1.83 (CI 121 to 126), ML 1.08 to 1.20 (MI 65 to 70), SL 1.10 to 1.21 (SI 52 to 59), EL 0.28 to 0.33, HFL 1.53 to 1.68 (FLI 92 to 97; FWI 20 to 21) mm. Head (Fig. 4) broad, with lateral margins divergent, and widest near vertex; posterior margin slightly concave mesad. Head with narrow, wavy longitudinal rugae, forming foveae behind level of ocelli and laterally; foveae feeble beneath head. Medial sulcus narrow but conspicuous beneath ocelli. Scrobes prominent, as in majors. Clypeus smooth, with projecting medial lobe as in major. Trunk (Fig. 5) irregularly rugose laterally (especially on propodeum), smoothest on anepisternum and pronotum. Dorsum with numerous foveae, and with rugae extending forward onto mesonotum from its posterior border. Posterior margin of scutellum with short, stout horns laterally. Propodeal spines short and stout, projecting caudad. Anterior peduncle of petiole short and deep; node of petiole broad, with lateral spines greatly shortened relative to worker castes. Postpetiole narrower than in workers, more than 50% wider than long in dorsal view. Petiole and postpetiole with

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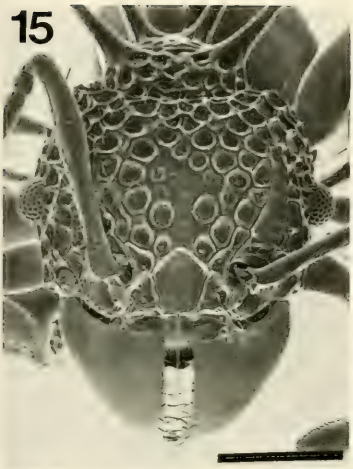
Figures 15–20. *Acanthomyrmex crassispina* from Botel Tobago (Taiwan). 15. Frontal view of head, minor worker. 16. Lateral view of trunk, minor worker. 17. Frontal view of head, major worker. 18. Lateral view of trunk, major worker. 19. Oblique dorsal view of postpetiole, minor worker. 20. Lateral view of waist, minor worker.

Scale lines. Figures 15–18, 0.50 mm. Figures 19–20, 0.10 mm.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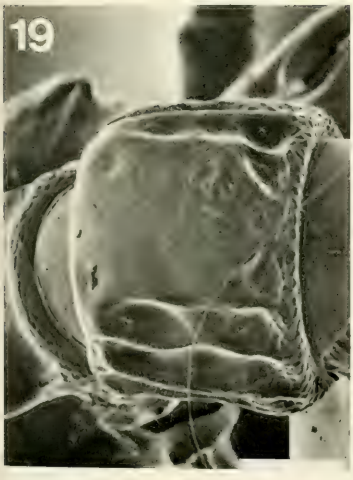
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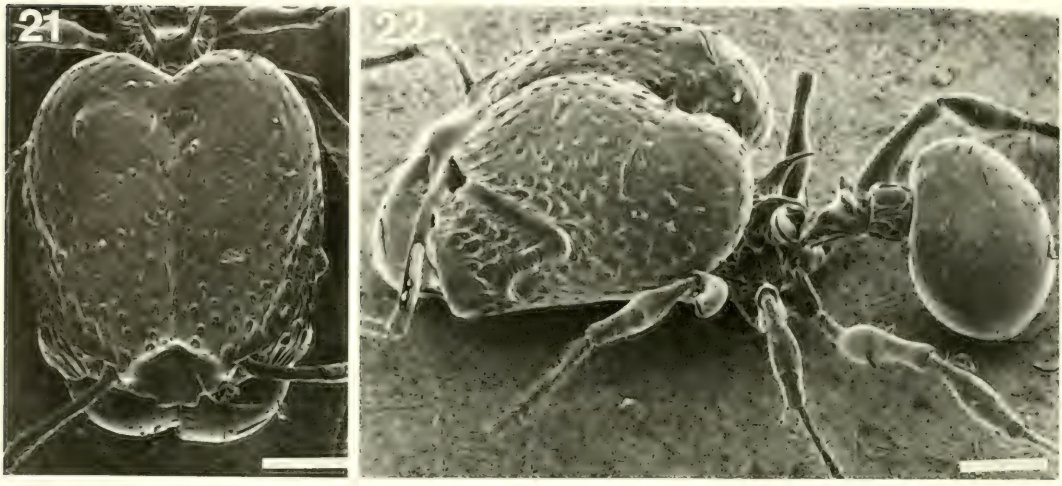

Figures 21–22. *Acanthomyrmex dusun* holotype (major worker). 21. Frontal view of head. 22. Dorsal-lateral view of trunk. *Scale lines.* 0.50 mm.

more pilosity than in workers, but otherwise pilosity similar to workers.

Male. Measurements of five specimens from southern Kalimantan (male from Peninsular Malaysia very similar): HW 0.93 to 1.03, HL 0.76 to 0.82 (CI 123 to 128), ML 0.46 to 0.51 (MI 56 to 64), SL 0.56 to 0.63 (SI 57 to 61), EL 0.30 to 0.32 mm. Head (Fig. 6) broad, widest immediately above eyes; vertex broad, posterior margin of head feebly concave. Head sculptured as in minor workers but less regular and much more feeble; pilosity long, rising 0.25 mm dorsally. Clypeus irregularly longitudinally rugose, forward margin lacks projecting lobes. Trunk (Fig. 7) as described for queen, but propodeal spines lacking; feebly and irregularly rugose dorsally with only traces of foveate sculpture. Both petiole and postpetiole with low, rounded nodes; postpetiole somewhat longer than wide in dorsal view. Jet black, with legs and gaster dark brown and mandibles dark yellowish orange.

Additional Records. MALAYSIA: *Peninsular Malaysia:* Selangor, Ulu Gombak Forest Reserve: 15 Feb. 1983, one minor worker (H. T. Imai, MCZ); 16 Feb. 1983, one minor worker (M. Kubota, MCZ); 7/10/1973, seven minors, one major, one dealate queen (B. Bolton, BMNH and MCZ); Universiti Malaya Field Studies Center, ca. 260 m, rainforest, no. H-385, 2 Aug. 1967, three minor workers (R. Crozier, MCZ). Kepong, Selangor, Forest Research Institute, 3 Feb. 1983, one minor worker (M. Kubota, MCZ); Pahang, below The Gap, ca. 850 m, hill forest, 17 Aug. 1967, two minor workers (R. Crozier, MCZ, BMNH); Perak, Ringlet Pass, 28 Feb. 1982, one minor worker (M. Kubota, MCZ). *Sarawak:* 4th Div., Gunung Mulu National Park, Kerangas, BMNH 1978-49, v–viii.1978, three minor workers, two majors, and one dealate queen (P. M. Hammond and J. E. Marshall, BMNH and MCZ); Gunung Mulu National Park, RGS Exped., Long Pala, lowland rainforest, soil

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Figures 23–28. *Acanthomyrmex ferox* from Kalimantan. 23. Frontal view of head, minor worker. 24. Lateral view of trunk, minor worker. 25. Frontal view of head, major worker. 26. Lateral view of trunk, major worker. 27. Dorsal view of postpetiole, minor worker. 28. Lateral view of waist, minor worker.

Scale lines. Figures 23–26, 0.50 mm. Figures 27–28, 0.10 mm.

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pocket on rock, 20/ix/1977, five minor workers and one major (B. Bolton, BMNH). *Sabah:* Gunung Silam, 440 m, no. A-12, 7 Jan. 1983, two minors and one major (R. Leakey, BMNH). INDONESIA: *S.E. Kalimantan (Borneo):* Pleihari-Martapura Reserve, lowland rainforest, nesting in leaf litter, 5 July 1983, 47 minor workers, two majors, seven males, and one dealate queen (M. W. Moffett and D. A. Fletcher, MCZ, BMNH, MCSN and MHN); 17–46 km W. Batulitjin, lowland rainforest, under bark of rotten stump, 2 July 1972, one minor worker (W. L. Brown, Jr., MCZ). *Sumatra:* Lampongs, Pedada-B. 22/I/1922, two minor workers (MCZ and BMNH).

Height of pilosity variable, with the longer hairs dorsally on the head extending about 0.15 mm in the syntypes and in the specimens from Kalimantan, Pahang (Malaysia) and the Gombak (Malaysia) specimen collected by Imai, but shorter (0.08 to 0.10 mm) in other series. Most of the workers with shorter cephalic pilosity have relatively sparse (and very short) pilosity on their gasters, and some also lack pilosity on their pronotal spines.

The traces of very fine rugulose sculpture present on the lateral surfaces of the mandibles of most *Acanthomyrmex* minor workers is generally absent in *A. ferox*, although this microsculpture can be discerned in the types. Petiolar node with spine length and curvature somewhat variable (Fig. 8D–E), PWI 105 to 143. Postpetiole of all major workers and some minors (i.e., those from Lampongs and Sarawak) with conspicuous foveae on node, as in individual in Figure 27. Femora sometimes more concave beneath than in syntypes, particularly in the Bolton specimens from Sarawak and the Perak (Malaysia) worker. Color in most specimens darker than in syntypes, reddish orange.

A. dyak minor syntypes (HW 1.00 and 1.04 mm) very similar to other *A. ferox* material; major syntype small (HW 2.28 mm), but not as small as the Sabah major (HW 1.98 mm); otherwise very similar to the Sarawak specimens described above. Tooth lacking at pronotal angle in both castes. Femora flattened or at most feebly concave beneath.

Natural History. A colony of nearly fifty workers was collected in southern Borneo nesting in leaf litter in disturbed primary rainforest (see Moffett, 1985).

Acanthomyrmex laevis new species
Figures 8F, 29–32; Map 1

Holotype. Minor worker deposited in MCZ from Peninsular Malaysia: Perak: Ringlet Pass, 28 Feb. 1982 (M. Kubota). Name refers to lack of sculpture on head.

Diagnosis. Very similar to *A. ferox*, but head of minor worker smooth, lacking all but traces of sculpture. Major worker unknown.

Minor. Holotype measures HW 1.03, HL 0.96 (CI 107), ML 0.80 (MI 83), SL 1.29 (SI 126), EL 0.21, HFL 1.42 (FLI 148; FWI 18) mm. Very similar in all respects to *A. ferox*, except head lacking sculpture dorsally and with only traces of rugae laterally and beneath head. The head sculpture is strongly developed in all *A. ferox* specimens, including one from the same locality as the *A. laevis* holotype.

In addition, the petiolar node of *A. laevis* (Fig. 8F) has somewhat longer petiolar spines than in *A. ferox* specimens, and the crotch between the spines is relatively narrow basally (in *ferox*, the crotch has a wide, convex base). A well-defined subpetiolar declivity is lacking, although a feeble declivity occurs. Node of postpetiole smooth (as in some *A. ferox*). Pronotal angle not forming a feeble tooth. Uniform dark orange red.

Additional Records. Known only from holotype.

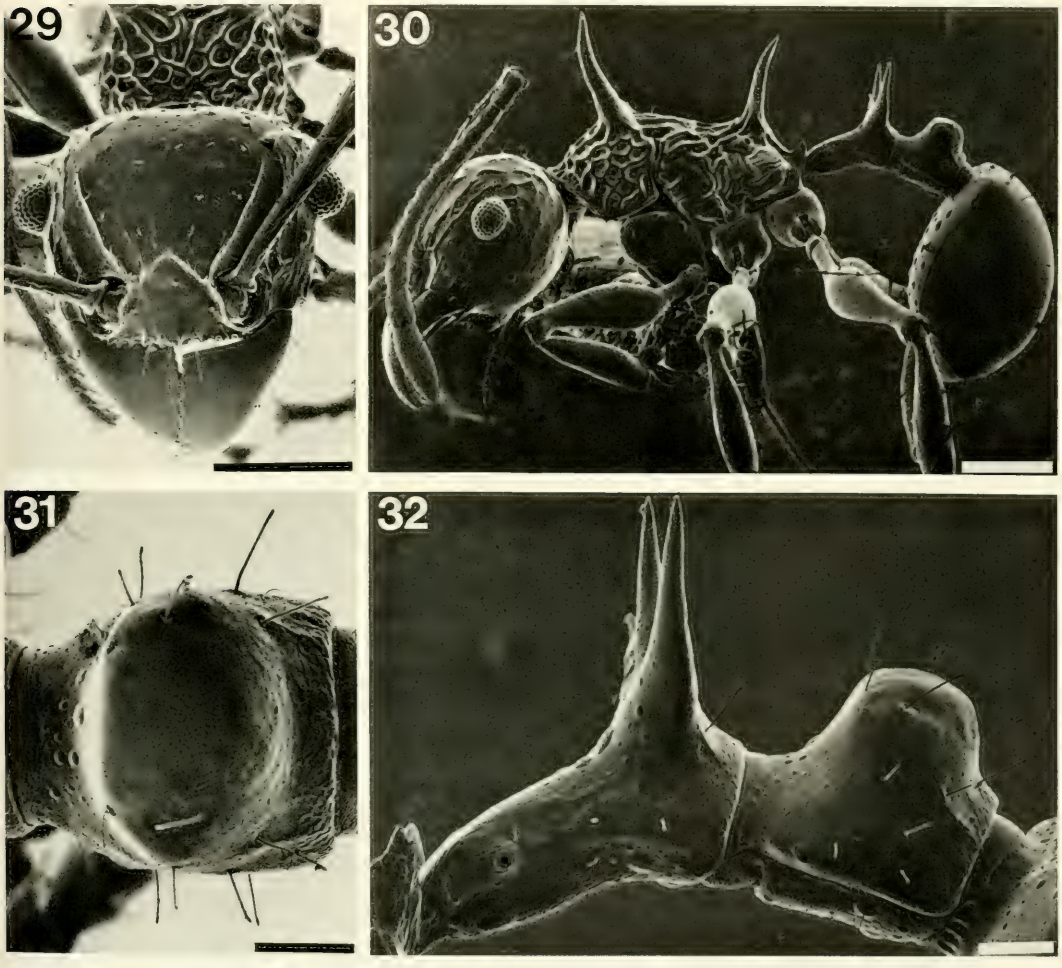
Acanthomyrmex luciolae
Figures 8G, 33–38; Map 1

Acanthomyrmex luciolae Emery, 1893: 245–246, pl. 6, fig. 5–10. Sri Lanka: Kandy, two minor workers and one major (E. Simon, MCSN and MHN [examined]).

Diagnosis. Minor workers with posterior margin of head deeply concave; head

of majors with conspicuous rugae. Propodeal spines long, slender, directed upwards rather than strongly caudad, and lacking a conspicuously thickened base; node of petiole without two long lateral spines. From Sri Lanka.

Minor. The two minor worker syntypes measure HW 1.10 to 1.11, HL 0.95 (CI 116 to 117), ML 0.79 to 0.83 (MI 83 to 87), SL 1.10 to 1.11 (SI 100), EL 0.22 to 0.23, HFL 1.21 to 1.26 (FLI 128 to 132; FWI 24) mm. When viewed in full-face, head strongly concave across posterior margin, and with moderately convex lateral margins. Maximum head width virtually the same above and below the level of the eyes. Head with rounded foveae having thick walls, except walls of foveae bordering on scrobes and on vertex are thinner, more like those of *A. ferox*; dorsally longest hairs extend about 0.18 mm. Clypeal index 111 and 113. Feeble lobe present on each side of medial clypeal hair; lateral clypeal hairs often in an enclosed fovea, although walls of fovea sometimes incomplete (as in Fig. 33). A well-devel-



Figures 29–32. *Acanthomyrmex laevis* holotype (minor worker). 29. Frontal view of head, at slightly oblique angle. 30. Lateral view of trunk. 31. Dorsal view of postpetiole. 32. Lateral view of waist.

Scale lines. Figures 29–30, 0.50 mm. Figures 31–32, 0.10 mm.

oped ruga extends back from each of these medial clypeal lobes, as described for *A. crassispina*. Mandibles lacking a ventral tooth.

Spines on trunk exceptionally long; pronotal spines straight and propodeal spines somewhat longer, slender and elegantly curved (Fig. 34). Pronotal spines with one to three conspicuous hairs. Pronotal angle not forming a feeble tooth. Propodeal declivity bordered on each side by two adjacent rugae, as described for *A. basispinosus*.

Petiole as in Figure 8G, PWI intermediate (67 to 70). Anterior peduncle of petiole long and narrow, with lateral hairs present, but sublateral hairs lacking; subpetiolar declivity present. Postpetiole much as described for *A. crassispina*, except hairier, and dorsum raised into a low node anteriorly, rather than evenly rounded in profile. Femora hairy, and with ventral surfaces only feebly concave. Color light orange yellow, legs yellow.

Major. Syntype measures HW 1.80, HL 1.83 (CI 98), SL 1.03 (SI 57), EL 0.26, HFL 1.26 (FLI 69; FWI 22) mm. Head sculpture as described for *A. ferox*, but costate sculpture on frons extending relatively farther back towards vertex, and foveae relatively feebler on sides of head. Without a distinct cephalic hollow. No darkly pigmented medial streak dorsad on head; wide medial sulcus conspicuous, low on face. Forward margin of clypeus without a medial projection. However, two feeble lobes are present, each with a single notch along their margins. Propodeal spine relatively short and virtually straight, in contrast to condition in the minor worker. Subpetiolar declivity lacking (although present in minor caste). Head and gaster a deeper orange than in minors.

Additional Records. SRI LANKA: Kandy, 600–700 m, nos. 1236 and 1240, VII/10–13/1955, two minor workers (E. O. Wilson, MCZ); Gilimale, 16–20 km NE of Ratnapura, nos. 1292, 1310, 1325, and 1354, VII/18–21/1955, six minor workers (E. O. Wilson, MCZ, BMNH). Several of the Wilson specimens have longer (up to 0.25 mm) pilosity on the head and relatively hairy pronotal spines; also some specimens lack the tibial spur usually present on the middle and hind legs of *Acanthomyrmex* ants. PWI 57 to 76. Most of these ants are darker and more red than syntypes.

The *notabilis* Group

Dorsal margin of the head of the majors at most very slightly notched mesad so that in full-face view margin appears rounded or somewhat flattened, but not strongly bilobed. Other characters: majors with propodeal spiracle opening slightly smaller and less conspicuous than in *luciolae* group; basal funicular segments relatively thick (width of the second and third funicular segments more than 25% greater than their average length in minor workers and less than 50% in majors), except in *A. notabilis*; hypostomal teeth often absent in majors. Dorsal surface of gaster invariably with very few (if any) long hairs.

All species in this group are from the Malay Archipelago; as yet none have been collected from the Asian mainland.

Acanthomyrmex careoscrobis new species
Figures 39A, 40–43; Map 2

Holotype. Minor worker deposited in BMNH from Malaysia: Sarawak: 4th Div., Gunung Mulu National Park, mixed dipterocarp forest, 200 m, pitfall trap, 14/III/1978 (N. M. Collins). Name derived from Latin *careo* + *scrobis*, referring to the lack of scrobes for retracted funiculi.

Diagnosis. Similar to *A. mindanao*, but lacking even a poorly developed funicular

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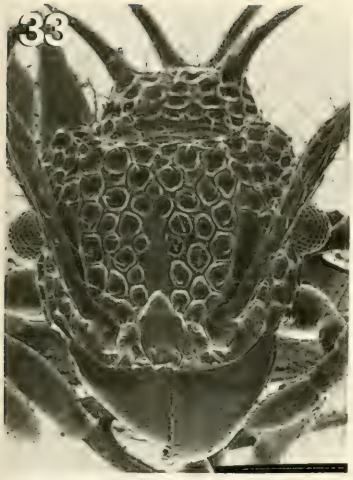
Figures 33–38. *Acanthomyrmex luciolae* from Kandy. 33. Frontal view of head, minor worker. 34. Lateral view of trunk, minor worker. 35. Frontal view of head, major worker. 36. Lateral view of trunk, major worker. 37. Dorsal view of postpetiole, minor worker. 38. Lateral view of waist, minor worker.

Scale lines. Figures 33–36, 0.50 mm. Figures 37–38, 0.10 mm.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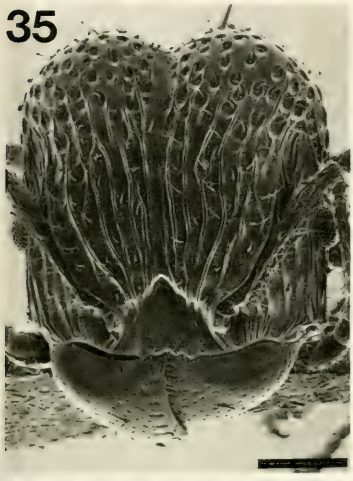
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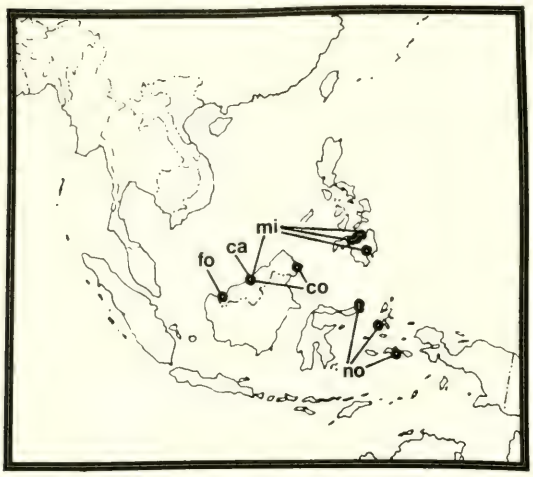


Map 2. Distribution of the species in the *notabilis* species group.

Abbreviations: ca = *A. careoscrobis*, co = *A. concavus*, fo = *A. foveolatus*, mi = *A. mindanao*, no = *A. notabilis*.

scrobe; without strongly projecting medial clypeal lobes. Major worker unknown.

Minor. Holotype measures HW 0.94, HL 0.79 (CI 118), ML 0.70 (MI 88), SL 0.80 (SI 86), EL 0.16, HFL 0.83 (FLI 105; FWI 24) mm. Head shape similar to *A. mindanao*, but slightly more deeply concave across posterior margin. Maximum head width virtually the same above and below the level of the eyes. Head with rounded foveae having thick walls; dorsally the longest hairs extend about 0.10 mm. Without any trace of grooves to retain retracted funiculi adjacent to scrobes for each scape. Scapes relatively short, barely overreaching back margin of head when retracted to scrobes. Clypeal index 178. Lobe to each side of medial clypeal hair feeble (essentially absent) and widely separated from the hair; lateral clypeal hairs apparently not in a completely enclosed fovea, but sculpture difficult to interpret. Smooth medial area of clypeus bordered by longitudinal rugae laterally. Mandibles lacking a ventral tooth.

Spines on trunk relatively longer than in *A. mindanao*, with pronotal spines in particular not as reduced in length. Pronotal spines with one hair or none. Pronotal angle not forming a feeble tooth. Propodeal declivity bordered on each side by a single rugum.

Node of petiole as in Figure 39A, PWI narrow (ca. 49). Anterior peduncle of petiole shorter and deeper than in *A. mindanao* and other species in the genus, and with lateral petiolar hairs present and sublateral hairs lacking; subpetiolar declivity present. Postpetiole (Fig. 42) similar to *A. mindanao*; with two pairs of hairs dorsally and two lateral pairs. Femora with scattered hairs throughout length, and with ventral surfaces distinctly concave; hind femora relatively short (FLI < 110). Orange yellow, with legs yellow.

Additional Records. Known only from holotype.

Acanthomyrmex concavus new species
Figures 39B–C, 44–47; Map 1

Holotype. Minor worker deposited in BMNH from Malaysia; Sarawak; 4th Div., Gunung Mulu National Park, RGS Exped., Long Pala, lowland rainforest leaf litter, 19/X/1977 (B. Bolton). Name refers to strongly concave posterior margin of head.

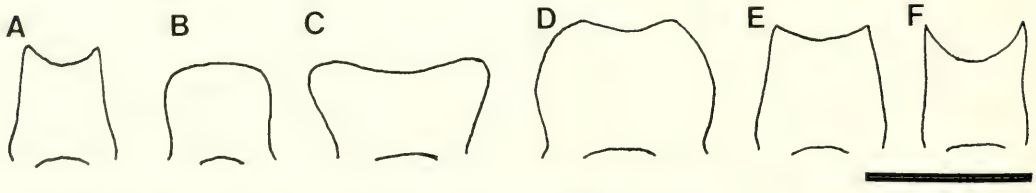
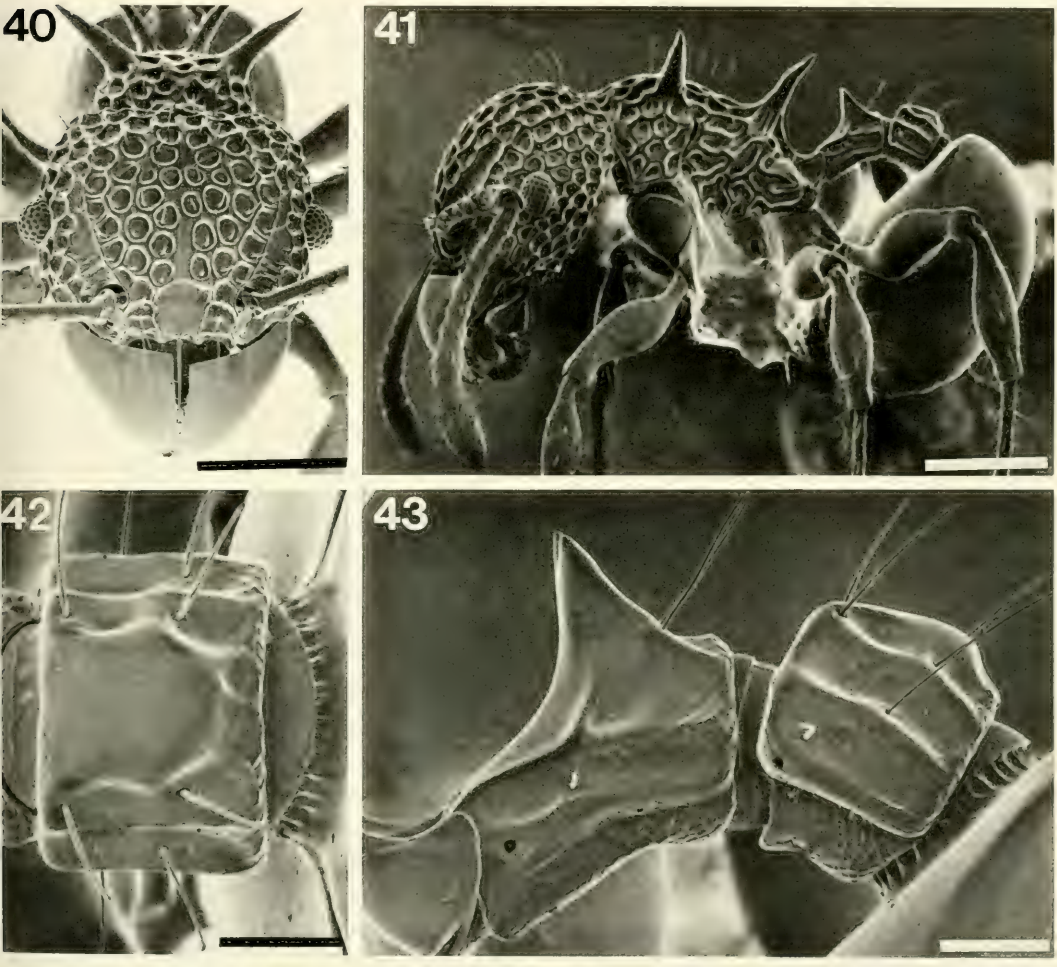


Figure 39. Petiolar nodes of minor workers in posterior view: *notabilis* species group. A. *A. careoscrobis* holotype; B. *A. concavus* holotype; C. *A. concavus* from Sabah; D. *A. foveolatus* holotype (major worker); E. *A. mindanao* paratype; F. *A. notabilis* from Sulawesi.

Scale line. 0.25 mm.

Diagnosis. Minors with head deeply concave dorsad and thus resembling *A. luciolae* and *basispinosus*, except: propodeal spines without a distinct thickened base, strongly directed caudad; mandibles each with a ventral tooth; medial clypeal lobes well-developed, projecting; postpetiole with only two pairs of hairs dorsally. Major worker unknown.

Minor. Holotype and single paratype measure HW 1.10, HL 0.90 (CI 122), ML 0.78 to 0.79 (MI 87 to 88), SL 0.90 (SI 82), EL 0.16 to 0.17, HFL 1.00 to 1.03 (FLI 111 to 114; FWI 24) mm. Posterior margin of head deeply concave in dorsal full-face view; head shape similar to *A. luciolae*, but with lateral margins of head less strongly convex. Head widest above the eyes. Head with rounded foveae having thick walls; dorsally the longest hairs extend 0.10 to 0.12 mm. Scapes short (SI < 90). Clypeal index 140 to 144. Lobe to each side of medial clypeal hair strongly produced, but widely separated from the



Figures 40–43. *Acanthomyrmex careoscrobis* holotype (minor worker). 40. Frontal view of head. 41. Lateral view of trunk. 42. Dorsal view of postpetiole. 43. Lateral view of waist.

Scale lines. Figures 40–41, 0.50 mm. Figures 42–43, 0.10 mm.

hair; lateral clypeal hairs in a completely enclosed fovea. Smooth medial area of clypeus not bordered laterally by rugae. Mandibles with a small but distinct ventral tooth.

Spines on trunk virtually straight, with propodeal spines extending more directly caudad than in other species; pronotal spines short, stubby, and lacking conspicuous hairs. Pronotal angle forming a feeble tooth. Sculpture on trunk particularly deeply impressed. Propodeal declivity transversely rugose, and bordered on each side by two adjacent rugae.

Petiolar node rounded, without dorsolateral teeth (Fig. 39B), so that PWI not measurable. Anterior peduncle of petiole long and narrow, and lacking lateral and sublateral hairs; subpetiolar declivity present. Postpetiole subrectangular, about one third wider than it is long, rounded dorsad and only feebly rugose on sides; with two pairs of hairs dorsally. Femora hairy, and with ventral surfaces distinctly concave; hind femora relatively short (FLI < 120). Color dark orange red, with legs and gaster lighter and more orange.

Paratypes. One minor worker, same collection data as holotype (MCZ).

Additional Records. MALAYSIA: *Sarawak:* 4th Div., Gunung Mulu National Park, camp 5, B.M. 1978-49, v–viii/1978, one minor worker (P. M. Hammond and J. E. Marshall, BMNH). *Sabah:* Gunung Silam, 330 m, no. A-6, 9/2/1983, one minor worker (R. Leakey, BMNH). The Sabah specimen has a distinctive, bilobed petiolar node (Fig. 39C).

Acanthomyrmex foveolatus new species
Figures 39D, 48–50; Map 2

Holotype. Major worker deposited in MCZ from Malaysia: Sarawak: Mount Poi, 200 ft. (E. Mjöberg). Name referring to cephalic sculpture.

Diagnosis. Major worker similar to that of *A. mindanao*, but with foveae on head very tiny and numerous. Minor worker unknown.

Major. Holotype measures HW 2.22, HL 2.49 (CI 90), SL 0.97 (SI 44), EL 0.22, HFL 1.16 (FLI 47; FWI 19) mm. Foveae on head numerous (even in vicinity of clypeus), very tiny and shallow (except for larger foveae along borders of antennal scrobes and beneath head, where foveae become confluent). Head virtually lacking pilosity. Cephalic hollow present but not as conspicuous as in *A. mindanao*. A darkly pigmented streak extends to hollow from dorsum of head; wide medial sulcus conspicuous from hollow to frontal area. Clypeal index 174. Forward margin of clypeus lacking a medial projection. Hypostomal teeth present.

Propodeal spines short, with distinctly thickened bases; bent caudad. Pronotal angle drawn out into a distinct tooth. Node of petiole without distinct dorsolateral denticles or spines (Fig. 39D), PWI narrow to intermediate (ca. 64). Anterior peduncle of petiole long and narrow, and lacking both lateral and sublateral petiolar hairs; subpetiolar declivity lacking. Postpetiole subrectangular, similar to that of *A. mindanao*; with only two pairs of hairs dorsally. Femora with scattered hairs, and with ventral surfaces distinctly concave. Orange yellow, with legs yellowish orange; head a richer orange and with contrasting yellow antennae.

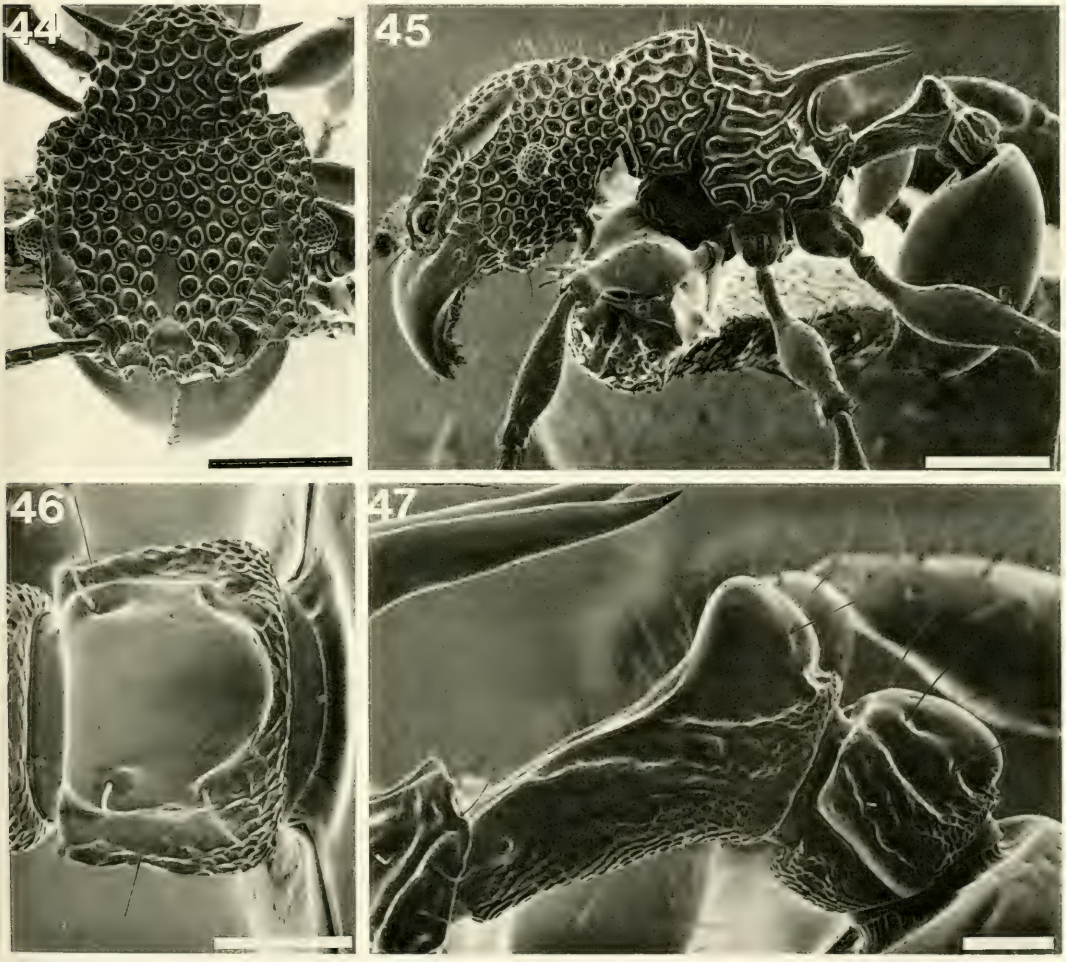
Additional Records. Known only from holotype.

Acanthomyrmex mindanao new species
Figures 39E, 51–56; Map 2

Holotype. Minor worker deposited in MCZ from Philippines: Mindanao: Davao Province, east slope of Mount McKinley, 3,300 ft., lot 33, under bark, 30 August 1946 (F. G. Werner). The specific name is a noun in apposition after the type locality.

Diagnosis. Postpetiole in both castes approximately cuboidal, not conspicuously wider than deep in dorsal view; propodeal spines shorter than in *A. notabilis*. Minors with posterior margin of head moderately concave in dorsal view, and with funicular scrobe present, although poorly developed; ventral mandible tooth usually present, and with strongly projecting medial clypeal lobes.

Minor. Holotype (HW 1.05 mm) and four minor paratypes measure HW 0.98 to 1.06, HL 0.84 to 0.91 (CI 114 to 117), ML 0.65 to 0.71 (MI 75 to 78), SL 0.83 to 0.88 (SI 81 to 84), EL 0.19 to 0.22, HFL 0.90 to 0.95 (FLI 104 to 107; FWI 21 to 22) mm. Head in full-face view appearing flattened or slightly concave across posterior margin. Head widest above the eyes. Head with oval foveae having thick walls; dorsally the longest hairs extend 0.08 to 0.10 mm. Scrobes bent sharply downwards posteriorly, forming a shallow groove for funiculus extending dorsad to each eye alongside groove for scape. Scapes relatively short (SI < 90), so that when retracted to scrobes, scapes barely extend beyond back margin of head. Mandibles often with relatively few denticles (usually eight or less; eight to 12 in most specimens in other species). Clypeal index 129 to 134. Lobe to each side of medial clypeal hair strongly produced, and more approximate to hair than in other



Figures 44–47. *Acanthomyrmex concavus* paratype (minor worker). 44. Frontal view of head. 45. Lateral view of trunk. 46. Dorsal view of postpetiole. 47. Lateral view of waist.

Scale lines. Figures 44–45, 0.50 mm. Figures 46–47, 0.10 mm.

species; lateral clypeal hairs not in a completely enclosed fovea. Smooth medial area of clypeus not bordered laterally by distinct rugae. Mandibles with a tiny but distinct ventral tooth.

Spines on trunk short relative to other species, propodeal spines conspicuously longer than pronotal spines, and are virtually straight to feebly curved caudad; pronotal spines very short and stubby (lacking in larger minor workers in some other series: see below). Pronotal spines without conspicuous hairs. Pronotal angle never drawn out into a feeble tooth. Propodeal declivity bordered on each side by one rugum or possibly two adjacent rugae (second rugum poorly developed when present).

Node of petiole as in Figure 39E, PWI narrow (45 to 64); caudal face of node usually with a pair of hairs near summit (absent in Fig. 56), in addition to the single pair found lower on the same face of node in this and most other *Acanthomyrmex*. Anterior peduncle of petiole relatively short and deep as in *A. notabilis*, and with lateral petiolar hairs present (but sometimes hair missing from one side of petiole); sublateral pair lacking. Subpetiolar declivity present. Postpetiole subrectangular, almost as long as it is wide in dorsal view, and with two or three longitudinal rugae on each side; hairy dorsally. Femora only with basal hairs or having one to three additional hairs, and with ventral surfaces distinctly concave; hind femora relatively short (FLI < 110). Orange yellow to reddish orange, with legs lighter yellow.

Major. Paratype measures HW 1.98, HL 2.16 (CI 92), SL 0.90 (SI 46), EL 0.26, HFL 1.00 (FLI 46; FWI 20) mm. Foveae on head smaller and shallower than in *A. notabilis* (somewhat larger and denser beneath head), numerous except very few present in area between antennal scrobes. Pilosity present on head, but more scattered than in *A. notabilis* majors. Cephalic hollow conspicuous. A darkly pigmented streak extends to hollow from dorsum of head; wide medial sulcus conspicuous from hollow to frontal area. Forward margin of clypeus with a medial projection. Hypostomal teeth absent. Propodeal spines short and curved caudad. Color as in minor workers, but head a richer orange, antennae a contrasting shade of yellow.

Paratypes. Four minor workers and one major, same locality data as holotype.

Additional Records. PHILIPPINES: *Mindanao:* Lanao District: Momungan, 6/20/1951, ten minor workers and one major (D. Empeso, MCZ and BMNH); Momungan, ser. B, 6/20/1951, thirteen minor workers (D. Empeso, MCZ); Olangon, 6/25/1951, eight minor workers (D. Empeso, MCZ, MCSN and MHN); Iligan, 1951, 29 minor workers (D. Empeso, MCZ); Ginoog, Misamis, Anakan Lbr. Co., 4/3/1935, nine minor workers (A. Reyes, MCZ). MALAYSIA: *Sarawak:* 4th Div., Gunung Mulu National Park, RGS Exped., Long Pala, lowland rainforest litter sample, 18.x.1977, three minor workers (B. Bolton, BMNH). The Philippine ants are very similar to the type series, except that the Momungan major is smaller (HW 1.64) and hairier than the paratype major. This major also has hypostomal teeth, and lacks a subpetiolar declivity. The Ginoog workers consistently lack the pair of hairs near the summit of the petiolar node which are usually present in specimens from other series. Color in a few specimens uniform yellow.

Workers of the Sarawak series are the smallest recorded for this genus (HW 0.70 to 0.76 mm), and are significantly smaller than any of the Philippine specimens (HW 0.90 to 1.11 mm). These ants lack a ventral mandibular tooth, lack sublateral hairs on their petioles, and have the pilosity on their postpetioles reduced to two pairs of hairs dorsally and one lateral pair.

The larger of the minor workers from the Philippines (HW > 1.05 mm) completely lack pronotal spines. Also, the same

Figures 48–50. *Acanthomyrmex foveolatus* holotype (major worker). 48. Frontal view of head. 49. Lateral view of trunk. 50. Lateral view of waist.

Scale lines. Figures 48–49, 0.50 mm. Figure 50, 0.10 mm.

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Figures 51–56. *Acanthomyrmex mindanao* paratypes. 51. Frontal view of head, minor worker. 52. Lateral view of trunk, minor worker. 53. Frontal view of head, major worker. 54. Lateral view of trunk, major worker. 55. Dorsal view of postpetiole, minor worker. 56. Lateral view of waist, minor worker.

Scale lines. Figures 51–54, 0.50 mm. Figures 55–56, 0.10 mm.

Figures 57–62. *Acanthomyrmex notabilis* from Sulawesi. 57. Frontal view of head, minor worker. 58. Lateral view of trunk, minor worker. 59. Frontal view of head, major worker. 60. Lateral view of trunk, major worker. 61. Dorsal view of postpetiole, minor worker. 62. Lateral view of waist, minor worker.

Scale lines. Figures 57–60, 0.50 mm. Figures 61–62, 0.10 mm.

individuals have better developed ventral mandibular teeth than in other minors; their gasters are somewhat hairier and they have a more deeply engraved frontal sulcus. They therefore show some characteristics intermediate between the minor and major castes.

Acanthomyrmex notabilis
Figures 39F, 57–62; Map 2

Pheidole notabilis F. Smith, 1860: 111, figs. 3–4. Indonesia: Moluccas: Batchian (i.e., Bacan Island), one minor worker and one major (A. R. Wallace, Hope Collection, University Museum, Oxford [examined]).

Acanthomyrmex notabilis—Emery, 1893: 244.

Diagnosis. Postpetiole of both worker castes narrow, much wider than deep in dorsal view; propodeal spines long; minors with head convex across posterior margin in dorsal view (except for very feeble medial concavity), without funicular scrobe, and with ventral mandible tooth lacking.

Minor. Syntype measures HW 1.01, HL 0.90 (CI 113), ML 0.73 (MI 82), SL 1.04 (SI 102), EL 0.17, HFL 1.13 (FLI 126; FWI 19) mm. Posterior margin of head convex in full-face view, although slightly flattened or with a trace of a concavity mesad. Maximum head width virtually the same above and below the level of the eyes. Head with rounded foveae having thick walls. As in *A. basispinosus*, short but conspicuous sulcus present mesad between the eyes above the frontal area. Dorsum of head with longest hairs extending about 0.12 mm. Scapes long, conspicuously overreaching back margin of head when retracted to scrobes. Clypeal index 117 (114 to 128 in other minor worker material). Lobe to each side of medial clypeal hair feeble or moderately developed; lateral clypeal hairs in a completely enclosed fovea. Smooth medial area of clypeus not bordered laterally by distinct rugae. Mandibles lacking a ventral tooth (at least in specimens other than holotype, as the undersurface of the mandibles is not accessible in the latter).

Spines on trunk long, somewhat curved caudad (straighter in most specimens from other series); propodeal spines slightly longer than those on pronotum. Pronotal spines without conspicuous hairs. Pronotal angle forming a feeble but distinct tooth in most specimens, but not in holotype. Propodeal declivity bordered on each side by two adjacent rugae, as described for *A. basispinosus* (*luciolae* group).

Node of petiole as in Figure 39F, PWI narrow to intermediate (79 in syntype, and 47 to 89 in eight specimens from other series). Anterior peduncle of petiole relatively short and deep, and lacking both lateral and sublateral petiolar hairs; subpetiolar declivity absent. Postpetiole narrow (almost twice as wide as it is long in dorsal view) and with a relatively raised node, and resembling that of *A. basispinosus*, although with only two pairs of hairs dorsally. Femora lacking all but basal hairs; ventral surfaces distinctly concave, particularly in the hind legs. Reddish orange to orange yellow, legs lighter.

Major. Syntype measures HW 2.25, HL 2.30 (CI 98), SL 1.11 (SI 49), EL 0.25, HFL 1.23 (FLI 54; FWI 20) mm. Relatively large, shallow foveae on head widely scattered dorsally (virtually lacking in area immediately above clypeus), denser laterally. Cephalic hollow present but indistinct. A darkly pigmented streak extends to hollow from dorsum of head; wide medial sulcus conspicuous from hollow to frontal area. Clypeal index larger than in minors, 138 in holotype. Forward margin of clypeus lacking a medial projection (although two very feeble, rounded lobes are sometimes present). Hypostomal teeth not accessible to view in holotype; usually present in other material. Propodeal spines moderately long and almost straight (generally not quite as long and usually curving somewhat caudad in other *notabilis* material). Pronotal angle lacking the feeble tooth characteristic of the minor caste. Anterior node of petiole generally deeper than in minors.

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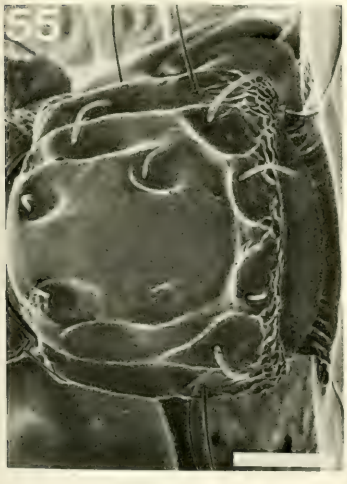
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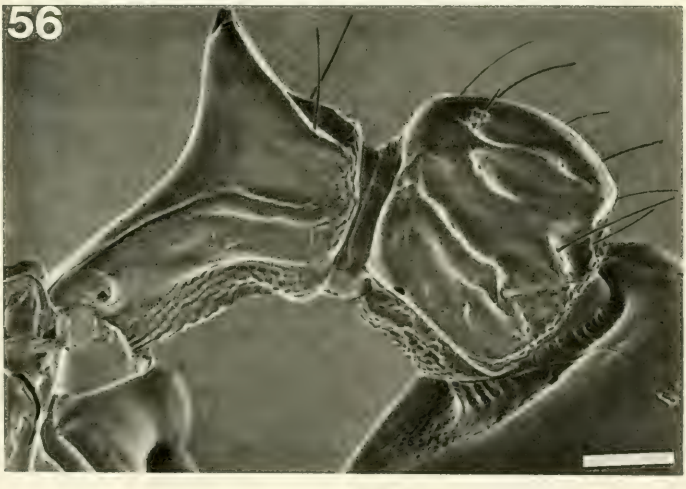
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Additional Records. INDONESIA: *Sulawesi:* SW slope of Mount Klabat, 400–600 m, rotten wood in rainforest, nos. B9-1, K-2, K-61, X-9, W1-7, and Y-22, 13–19/VI/1972, 24 minor workers and nine majors (W. L. Brown, Jr., MCZ and BMNH); Air Madidi slope of Mount Klabat, 400–600 m, rotten wood in wet forest, nos. H3-6 and L-8, 13–19/VI/1972, 13 minor workers and two majors (W. L. Brown, Jr., MCZ and BMNH); Tangkoko-Batuangus Reserve, 200 m, nesting in log in rainforest, 29 July 1983, 37 minor workers and three majors (M. W. Moffett and D. A. Fletcher, MCZ, BMNH, MCSN and MHN). *Seram:* above Haruru, near Masohi, 50–150 m, rotten wood in rainforest, no. M-122, 18 March 1981, 12 minor workers (W. L. Brown, Jr., MCZ and BMNH). Seram minor specimens tending to be somewhat smaller than those from Sulawesi (HW averaging [$\bar{X} \pm$ SE] 1.13 $\pm$ 0.04 mm, versus 1.02 $\pm$ 0.04 mm for the Sulawesi minors; samples of 36 and 7 minors, respectively).

Natural History. The ants nest in cavities within logs in primary rainforests. Nests typically contain stores of fig seeds and other tiny seeds (see Moffett, 1985).

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LITERATURE CITED

EMERY, C. 1893. Formicides de l'ile de Ceylan. Ann. Soc. Ent. Fr., **62:** 239–255.

———. 1909. Expedition de la Nouvelle-Guinea 1904–05. Nova Guinea, **8:** 249–259.

———. 1922. Hymenoptera. Family Formicidae, subfamily Myrmicinae. *In* P. Wytsman (ed.), Genera Insectorum, fasc. 174, V. Verteneuil and L. Desmet, Brussels. 397 pp., 7 pl.

HARRIS, R. A. 1979. A glossary of surface sculpturing. Occasional Papers in Entomology, California Dept. Food and Agriculture, no. 28, 31 pp.

HENDY, M. D., AND D. PENNY. 1982. Branch and bound algorithms to determine minimal evolutionary trees. Math. Biosc. **59:** 277–290.

KUGLER, C. 1978. A comparative study of the myrmicine sting apparatus. Studia Ent., **20:** 413–548.

MOFFETT, M. W. 1985. Behavioral notes on the Asiatic harvesting ants *Acanthomyrmex notabilis* and *A. ferox*. Psyche, **92:** 165–179.

SMITH, F. 1860. Descriptions of new species of hymenopterous insects collected by Mr. A. R. Wallace at Celebes. J. Proc. Linn. Soc. London Zool., **5:** 57–136.

WHEELER, G. C., AND J. WHEELER. 1954. The ant larvae of the myrmicine tribe Myrmecinini. Proc. Entomol. Soc. Washington **56**(3): 126–138.

———. 1977. Supplementary studies on ant larvae: Myrmicinae. Trans. Amer. Entomol. Soc., **103:** 581–602.

———. 1983. Supplementary studies on ant larvae: Myrmicinae. Trans. Amer. Entomol. Soc., **108:** 601–610.

WHEELER, W. M. 1919. The ants of Borneo. Bull. Mus. Comp. Zool. Harvard, **63**(3): 43–147.

———. 1930. Formosan ants collected by Dr. R. Takahashi. Proc. New England Zool. Club, **11:** 93–106.

WILSON, E. O. 1985. Ants of the Dominican amber (Hymenoptera: Formicidae). 1. Two new myrmicine genera and an aberrant *Pheidole*, Psyche, **92**(1): 1–9.

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The Neotropical Orb-weaver Genera *Chrysometa* and *Homalometa* (Araneae: Tetragnathidae)

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Ornithological Gazetteers of the Neotropics (1975–).

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THE NEOTROPICAL ORB-WEAVER GENERA *CHRYSOMETA* AND *HOMALOMETA* (ARANEAE: TETRAGNATHIDAE)

HERBERT W. LEVI[1]

ABSTRACT. *Chrysometa* and *Homalometa* are neotropical members of the family Tetragnathidae. Tetragnathidae are separated from Araneidae by the configuration of the male palpal parts, the large tarsal organ on the cymbium and the cone-shaped palpal tibia. The female epigynum is flat rather than three-dimensional, often with complicated internal ducts; or rarely, the epigynum is absent. The abdomen's integument is often underlain by evenly sized white or silver spots. Relative to body size, males have longer chelicerae than females. Tetragnathid males when mating hold females some distance from themselves. In many species the femoral-patellar joint is extended in resting position.

There are 127 known species of *Chrysometa*, 94 of them new; there are three species of *Homalometa*, two of which are new. Most *Chrysometa* species occur at high altitudes in the Andes and in paramos (both poorly collected areas); only a few species are known from low elevation rain forests.

INTRODUCTION

The study of *Chrysometa* was triggered by numerous inquiries from ecologists and collectors needing help with determinations. Unlike many other orb-weaver genera, *Chrysometa* is not readily recognized by ecologists or even by knowledgeable araneologists. While some *Chrysometa* species are found in low altitude forests and others at intermediate elevations, many are found at and above timberline. The mountains of Central America have proved unexpectedly rich in *Chrysometa* species, especially at higher elevations. The paramos of the Andes may have three or four species living sympatrically. The high altitude species are puzzling, since no two populations are quite alike. Is each population a separate species or does each represent a geographic form within a variable species?

The placement of the metines, which include *Chrysometa* and *Homalometa*, has been controversial. Orb-weaver genera related to *Meta* are found in all parts of the world; the diversity appears greatest in the Indopacific. In American literature they have been placed in the subfamily Metinae of the family Araneidae. Brignoli (1983) separated the metids as a distinct family. Other authors, however, have recognized a relationship between the metines and the tetragnathids. Simon (1895, 1929) placed the group in the subfamily Tetragnathinae of his family Argiopidae. More recently, Locket, Millidge and Merrett (1974) placed *Meta* of Great Britain in the Tetragnathidae, along with *Tetragnatha* and *Pachygnatha*. In the present treatment I have also placed the metines in the Tetragnathidae, though I still have some doubts about the distinctness of this family. In my past revisions of nearctic non-cribellate orb-weavers, all the genera were placed in one family (Levi, 1974, 1980a, 1981). Once it was recognized that the orb-web is a primitive character of web spiders (Levi, 1980b; Coddington, 1986), it could no longer be used as a synapomorphy to combine the araneids and tetragnathids; consequently, the relationship of the two groups required further investigation. The distinctive specialized (autapomorphic) features needed to define the family Tetragnathidae are still not satisfactory. However, as revisors remove erroneously included genera from Araneidae, the family becomes easier to define.

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I wish especially to thank Paul Hillyard. Not only does the British Museum have the largest number of types, but some specimens were requested a second time after I realized that it was essential to take off the epigynum to examine the internal genitalia.

C. Craig, W. Eberhard, and J. A. Kochalka supplied many specimens with valuable habitat notes. J. Coddington supplied notes and photographs, read part of the manuscript, and made improvements. W. Eberhard, W. Maddison, B. Opell, and F. Vollrath read the introduction and made corrections and valuable suggestions. C. Villars, L. Levi, and C. Bui improved the wording.

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METHODS

In addition to the usual examination (Levi, 1985), temporary slide mounts were made of the female epigyna with Hoyer's medium (Krantz, 1978) between two cover glasses. This was done in order to see the internal ducts that often appear on the outside as diagnostic dark marks around the sculptured part of the epigynum. In spite of this examination by compound microscope, the course of ducts in many species was not completely determined; they are among the most complex orbweaver ducts examined. Their morphology is a special problem beyond the scope of this revisionary study. After examination, each epigynum was removed from the microscope preparation and placed in a small vial along with the specimen from which it came.

After completing my previous orbweaver studies, I sorted other available collections and attempted to determine the additional specimens, using the newly-

made illustrations and keys to test their adequacy. With this group, however, there were so few specimens for so many species that the test could not be done. Consequently, I am less certain of species limits than I would like to be.

Many new species are described from a single individual. Taxonomists of many animal groups consider this poor procedure. Nevertheless, many North American spider species have been named from a single individual and other specimens were found subsequently.

FAMILY TETRAGNATHIDAE Menge, 1866

Tetragnathidae Menge, 1866: 90. Type genus for the family, *Tetragnatha*.

Simon (1895) placed the genus *Meta* and its relatives into the Tetragnathinae, which he considered a subfamily along with the Linyphiinae, Nephilinae, Argiopinae, Theridiosomatinae, Arciinae, and others. In his posthumous *Araignées de France* (1929), Simon again placed *Meta* in the subfamily Tetragnathinae. This was followed by Locket, Millidge, and Merrett (1974), who placed the European metids into the Tetragnathidae. In the absence of specialized characters that might set apart the Tetragnathidae, I have been reluctant to consider them separate from the Araneidae. While more characters are known that define Tetragnathidae, most are plesiomorph, or it is difficult to ascertain whether they are specialized or left over from the past. (However, the family Araneidae has several good apomorphies.) This revision did not resolve the problem, but perhaps my forthcoming study on the remaining members of the neotropical Tetragnathidae will.

Kaston (1948) separated Tetragnathidae from Araneidae by the presence of trichobothria on the femora of the legs, by the absence or rudimentary nature of the boss on the chelicerae, and by the large and powerful chelicerae in most species. He included only *Tetragnatha*, *Pachygnatha* and *Glenognatha*, the New England representatives. According to Kaston, *Meta* lacks these diagnostic trichobothria; Metinae have smaller chelicerae, with a cheliceral boss. However, the relatively simple genitalia which characterize *Tetragnatha* and *Meta* relatives might provide better diagnostic and synapomorphic features.

The nearctic and neotropical genera which belong in the Tetragnathidae are *Tetragnatha*, *Pachygnatha*, *Glenognatha*, *Cyrtognatha*, *Dolichognatha*,[2] *Leucauge*, *Azilia*, *Metabus*, *Meta*, *Metellina*, *Metleucauge*, *Chrysometa*, *Homalometa*, and probably also *Nephila*, *Nephilengys*, and *Zygiella*. Numerous other genera probably also belong here: *Alcimosphenus*, *Metargyra*, and *Opadometa* appear close to *Leucauge*, *Hispanognatha* close to *Glenognatha*. They will be reexamined at a later time, when I revise the neotropical *Leucauge*, *Azilia*, *Glenognatha*, *Tetragnatha*, and related genera. The family is probably closest to the Araneidae. In the past, *Tetragnatha*, *Pachygnatha*, *Glenognatha*, *Dolichognatha*, and *Leucauge* have been considered tetragnathids; *Nephila*, *Herennia*, and *Nephilengys* nephilines (Araneidae); *Zygiella* araneine; and the others metines (Araneidae) (Roewer, 1942).

RELATIONSHIPS

Discussed below are the characters that, in addition to those published earlier (Levi,

[2] Forster and Platnick (1984: 5) complained that I (1981: 277) synonymized *Landana* with the genus *Dolichognatha* "on phenetic grounds." They apparently overlooked that all species of *Dolichognatha* share synapomorph characters (Levi 1981: 278). They further complained that in 1981 I excluded archaeids from the Araneoidea while in my 1982 encyclopedia article archaeids were wrongly included. Instead of charging that I changed my mind in the wrong direction, Forster and Platnick might well have ascertained the chronology. (The direction of changes is of importance to evolutionary biologists.) The encyclopedia article (obviously not a "new" classification but merely an eclectic summary) was written in 1978 on short notice without opportunity to revise it before publication. The 1981 revision was prepared in 1979 and 1980, and conclusions published there still hold.

1980a), distinguish the tetragnathids from the araneids. I am more concerned here with the distinction between these two families (Tables 1, 2) than the placement of theridiids and linyphiids. There seems no clear distinction between the metines and the remaining tetragnathids.

1. Locket *et al.* (1974: 61) described the palpus of metines as having a long embolus lying between two sclerites originating from the tegulum. The conductor (C in Figs. 18–22) is flattened and curved; the other sclerite appears to arise from the base of the embolus and is the terminal apophysis (A in Figs. 18–22). The authors believe, and I agree, that the simplicity of structure resembles that found in *Tetragnatha*. *Tetragnatha*, however, lacks the terminal apophysis. (A terminal apophysis is shown in Locket *et al.*, 1974, fig. 36d; I may have considered the structure part of the conductor.) This contrasts with the more complex palpus found in the Araneidae, where a median apophysis functions to engage the scape of the female epigynum.

In *Dolichognatha* (Levi, 1981, figs. 13, 15) and in *Meta* (Levi, 1980a, fig. 124) there is often a lateral apophysis at the base of the embolus, which appears to be homologous with the terminal apophysis found in all *Chrysometa* (A in Figs. 18–22). *Metleucauge* has a similar sclerite between embolus and conductor which is free (Levi, 1980a, figs. 148–150) and which previously had me puzzled; undoubtedly it is also homologous with the terminal apophysis in *Chrysometa*. The males of tetragnathines and metines always lack the prominent radix found in palpi of all Araneidae (R in Levi, 1985, figs. 6–9), and usually lack a median apophysis (M in Levi, 1985, figs. 6–9).

In several tetragnathid genera the embolus is wrapped in the conductor (Table 1; Figs. 18–22), otherwise an uncommon feature of the Araneoidea and perhaps a synapomorphy. *Tetragnatha*, *Pachygnatha* and the metines have a spherical tegulum (T in Figs. 18–22) with the conductor, the embolus, and the terminal apophysis sitting apically on the bulb of the palpus (Figs. 16, 17), rarely ventrally. This configuration and the position of embolus, conductor and terminal apophysis (when present) are apomorphies. They are not found in other Araneoidea.

In tetragnathids the cymbium of the palpus is a spoon-shaped structure located dorsally to the bulb (Figs. 16, 17); this position is also characteristic of most spiders and thus plesiomorphic. In the Araneidae, however, as a result of a twist of cymbium and bulb, the cymbium appears on one side of the palpus, towards the midline of the spider, and the dorsal position is occupied by the tegulum and subtegulum (Y in Levi, 1985, figs. 6–9). In the Tetragnathidae the cymbium may become modified; the tendency to be modified in various ways is perhaps an autapomorph character for the family. For example, in *Tetragnatha* the cymbium is reduced (Levi, 1981); in *Chrysometa* it is not reduced, but has a dorsal apophysis on its base (Figs. 17, 21); in *Homalometa* (Figs. 736, 745) it is much reduced and modified. The paracymbium (P in Figs. 16, 17, 21) is usually present and large; it may be a free structure (*Tetragnatha*, *Pachygnatha*, *Chrysometa*) or attached to the cymbium (*Meta*, *Metellina*). It is absent in *Homalometa*. In the Araneidae and Theridiidae it is unusual for the cymbium to be modified. Only in some Araneidae is the paracymbium a large structure (e.g., *Micrathena*, Levi, 1985, figs. 710, 711). The homology of these modifications is, of course, uncertain.

The sperm duct inside the tegulum is variable, short in some tetragnathid genera, long in *Chrysometa*, long and convoluted in *Azilia*, *Metabus*, and *Nephila*. This might be of importance and will be investigated further. Gerhardt (1923) observed that in *Leucauge* and *Tylorida* (a South Pacific metine), but not in araneids, the sperm duct is strengthened by ribs or punctuations.

An easily visible character of Tetragnathidae is the large tarsal organ present near the tip of the cymbium of the male palpus

(Levi, 1980a, figs. 174, 199). Though present on the cymbium of many Araneidae species, this structure is smaller and often hidden by more dense setation. Although scanning electron micrographs were made, no distinctive features other than size were found on tetragnathid or araneid tarsal organs. The presence of a large tarsal organ in tetragnathids is probably also a plesiomorph character, since a prominent tarsal organ is present on the palpal tarsi of juvenile and female spiders.

2. It may well be that the most characteristic feature of the family Tetragnathidae, and perhaps an autapomorph character, is the cone-shaped tibia of the male palpus with its distal rim slightly modified (but not sclerotized) to fit the cymbium (Fig. 16). This tibia resembles the palpal tibia of theridiids, except that the theridiid tibia has an entire distal rim. The cone-shaped male palpal tibia may be a synapomorphy of tetragnathids and theridiids. In araneids, the palpal tibia is a shallow saucer with humps (Levi, 1985, figs. 16, 310). An exception among the Araneidae is the recently described male of *Sedasta* (Ledoux, 1985), which has a cone-shaped tibia.

The length and shape of the palpal tibia are related to the mating position of the spider (Gerhardt, 1921, 1923, 1933). In *Tetragnatha* and *Pachygnatha* (and presumably also in *Glenognatha*) the female and male face one another and engage chelicerae. In *Tetragnatha*, the abdomen of the female folds under, permitting the male's long palpal articles to reach the female genital opening (Gerhardt, 1921, pl. 3, fig. 4; Levi, 1981, pl. 4). In *Pachygnatha*, male and female raise the front of their carapaces and hold their abdomens down, venters parallel (Gerhardt, 1921, pl. 3, fig. 5. The strong coupling of the chelicerae, without doubt an autapomorphy of these two genera, is probably related to the absence of an epigynum in these groups. The mating position of *Meta* and *Zygiella* differs in that the chelicerae do not engage. Facing each other at first, male and female "fold down" to a venter-to-venter position facing the same direction in loose embrace (Gerhardt, 1933), permitted by the relatively long tibiae. Eberhard (personal communication) has photographs of *Leucauge mariana* mating and probably clasping chelicerae. In contrast, almost all Araneidae species mate on a mating thread in a tight embrace (Gerhardt, 1933; Robinson and Robinson, 1980). Such tight clasping would be difficult if the palpal tibiae were long. Helverson (1976) correctly points out that, while courtship differs from species to species, the mating position is a more conservative character.

Sperm induction, duration of palpal insertion, and number of hematodochal contractions during mating differ among species and genera of Tetragnathidae but are relatively constant in the Araneidae. In the genera *Tetragnatha* and *Pachygnatha*, according to Gerhardt (1921, but first seen by Menge, 1866: 92), both the conductor and the embolus are inserted into the female genitalia; in all other spiders, as far as is known, only the embolus is inserted.

3. The secondary eyes have a canoe-shaped tapetum and are closely grouped, both plesiomorphic characters of the family Tetragnathidae. If the eyes are spread out, the laterals distant from the medians, then the clypeus height is more than twice the diameter of the anterior median eyes (*Tetragnatha*, *Nephila*), and the secondary eyes may have lost the tapetum entirely (all secondary eyes of *Tetragnatha* and *Azilia*, and the posterior median eyes only of *Pachygnatha*). This is a synapomorph character of these genera, but a poor one because it involves loss. If the tapetum of the posterior median eye is reduced, the narrow "canoe" moves to the median of the spider (some *Chrysometa* species). In Araneidae, by contrast, the clypeus is usually low (there are exceptions), and the posterior median eyes have the canoe-shaped tapetum narrow, positioned laterally, with loops of rhabdoms toward the median (Levi, 1978, figs. 4, 5).

4. In most Tetragnathidae the chelic-

erae of the male are larger than those of the conspecific female. Exceptions are *Meta menardi*, species of *Azilia* and *Homalometa*. Males with enlarged chelicerae are found in many theridiids and linyphiids. The males of most species of Araneidae have smaller, weaker chelicerae than females.

5. The endites are relatively longer than those of Araneidae and are distally widened.

6. In resting position, the femoral-patellar joint of the anterior legs is held straight (Levi, 1980a), as is the case with many uloborids and dinopids; *Dolichognatha* is an exception. *Chrysometa* may be another (W. Eberhard, personal communication, Plate 2). Most araneids rest with the femoral-patellar joint flexed.

7. The surface of the epigynum, when present, usually lacks the three-dimensional sculpturing found in Araneidae, and the epigynum may be reduced or lacking (see above) (*Meta*, *Metellina*, *Pachygnatha*, and *Tetragnatha*). The epigynum of linyphiids and theridiids is also a relatively flat structure.

8. Species of Tetragnathidae commonly have the abdomen underlain by silver or white spots. Silver spots are relatively uncommon in Araneidae; they are found in *Argiope*. In the Theridiidae, silver spots are found in *Argyrodes* and *Thwaitesia*; in linyphiids they are also less common.

9. Perhaps the most illuminating discussion of the similarities between Metinae and Tetragnathinae was made by Wiehle (1967) and is based mainly on European species. Some of Wiehle's statements, however, could not be confirmed. The sperm of *Meta* and *Tetragnatha* has a spherical head and a tail like that of pholcids and *Atypus*, while Araneidae and Theridiidae have peg- or pencil-shaped sperm. We do not currently know the shape of sperm in related families; sperm shape in *Meta* and tetragnathids may be a plesiomorph condition. Here, he fails to cite any reference. An earlier paper by Tuzet and Manie (1959) pictures the sperm head of *Nuctenea cornuta* as oval to spherical, and that of *Tetragnatha pinicola* as elongate or pencil-shaped.

Another character mentioned by Wiehle is that the eggs of *Meta* (and *Tetragnatha*) are not agglutinated as are those of *Araneus*. In *Meta* the eggskin is only partly shed and covers part of the abdomen and leg tips for a day, after which it is shed in the first molt along with the exuvia (Holm, 1940). Nonagglutination is presumably a plesiomorph condition. Data provided by Kaston (1948) indicate that the agglutination of eggs cannot be generalized; it is not the same in related species.

Wiehle (1967) discusses the lack of fertilization ducts in the epigynum of *Meta* and *Metellina*, and the complete absence of the epigynum in *Tetragnatha*. However, fertilization ducts, sclerotized ones at that, are present in both *Chrysometa* and *Homalometa*. We can only conclude that the internal parts of the female copulating structures are unusually variable in the family Tetragnathidae.

10. A number of important and consistent differences in the behavior of Tetragnathidae and Araneidae have recently been cited by Eberhard (1982). He found no distinct differences between species that had been placed in the metines and tetragnathid species. Eberhard includes observations on more than eight species in five genera of tetragnathines, more than seven species in five genera of metines, and more than 50 species in 28 genera of araneines, as well as anapids and uloborids. The many species observed include species of *Meta*, *Chrysometa*, *Metabus*, and *Leucauge* which made the same web-building movements as species of *Dolichognatha*, *Tetragnatha*, *Azilia*, and *Glenognatha* (tetragnathines), but not the same as members of the Araneidae.

Although the main features of web construction were the same in the five groups (tetragnathines, metines, araneids, anapids, and uloborids), there were slight differences in orb-web construction and wrapping behavior. The first difference cited is that of locating sticky spiral at-

TABLE 1. MALE PALPAL CHARACTERS THAT SEPARATE THE FAMILY TETRAGNATHIDAE FROM THE ARANEIDAE.†

Taxon	a	b	c	d	e	f	g	h
Tetragnathidae								
Tetragnatha	+	L	+M	+	S	–	–*	W
Pachygnatha	+	L	+M	+	S	–	–	W
Glenognatha	+	L	+M	+	S	–	–	W
Dolichognatha	+	–	–M	+	C	–	L	S
Leucauge	+	–	–H	+	C	–	–	W
Azilia	+	–	–M	+	C	–	–	–
Meta	+	–	–M	–	C	–	L	W
Metellina	+	–	–M	–	–	–	L	W
Metleucauge	+	–	–M	+	C	–	A	S
Chrysometa	+	+	+M	+	C	–	L	W
Homalometa	+	L	A	–	?	?	?	?
Nephila	+	–	–H	+	C	–	–	W
Zygiella	+	–	±M	–	–	R, M	L	S
Araneidae								
Argiope	–	–	–H	–	–	R, M	–	S
Araneus	–	–	–H	–	–	R, M	H	S
Micrathena	–	–	–M	–	–	R, M	A	S

† a. Cymbium dorsal (+), cymbium mesal (–); b. Cymbium modified by being lobed (L) or having an apophysis (+), not modified (–); c. Paracymbium a free sclerite (+), attached to cymbium (–), absent (A). Paracymbium large, modified and sculptured (M), a small hook (H); d. Tegulum spherical with sclerites apical (+), sclerites on face of tegulum (–); e. Sperm duct in tegulum coiled (C) or swollen (S) of about equal diameter within tegulum, not coiled (–); f. Radix present (R), median apophysis present (M), both sclerites absent (–); g. Terminal apophysis a lobe from base of embolus (L), a free sclerite (A), separated by distal hematodocha (H), absent (–). *Part of what I considered the conductor (Levi, 1981) may be terminal apophysis (Locket *et al.*, 1974, fig. 36d); h. Length of embolus supported (S) by or wrapped in conductor (W), conductor absent (–).

tachment points. Tetragnathids including metines (and also in theridiosomatids, anapids, and mysmenids, J. Coddington, personal communication) tap forward with the inside leg I and araneids tap sideways with the outside leg I. However, some *Chrysometa* species have been observed making both tetragnathid and araneid movements. Eberhard (1982) gives reasons why he considers the tetragnathid movements primitive, but does not consider the uloborids or the dinopids as outgroups.

The second behavioral difference is the spider's contact with the temporary spiral when starting to lay down the sticky spiral. Tetragnathids, including metines (and theridiosomatids, anapids, and mysmenids, J. Coddington, personal communication), lose contact. The spiders move beyond the outermost loop of the temporary spiral, completely out of contact with it when attaching the outermost sticky spiral. Araneids all maintain contact. Eberhard could not decide which behavior was primitive and which derived.

Tetragnathids, including metines, usually attack-wrap prey without rotating before biting, or slowly rotate prey after cutting it free of the web.[3] Araneids usually attack-wrap their prey, rotating it like a spitted animal in a rotisserie, before biting. (Attack-wrapping is not used with some prey and is never found in some genera, e.g., *Gasteracantha, Micrathena, Mastophora, Dicrostichus, Poecilopachys, Celaenia* and *Nephila*. It may be a loss or a primitive condition.)

Some tropical *Tetragnatha* and *Glenognatha*, however, differed from metines

[3] This behavior was reversed in Eberhard (1982) (Eberhard in letter, 1985).

TABLE 2. CHARACTERS THAT SEPARATE THE FAMILY TETRAGNATHIDAE FROM THE ARANEIDAE.†

Taxon	2	3	4	6	7	8	10
Tetragnathidae							
Tetragnatha	+	L	+	+	L	+	+
Pachygnatha	+	L	+	+	L	+	?
Glenognatha	+	L	+	+	L	+	+
Dolichognatha	+	+	+	−	+	+	+
Leucauge	+	+	S	?	+	+	+
Azilia	+	L	S	?	+	−	+
Meta	+	+	S	+	−	−	+
Metellina	+	+	+	+	+	+	?
Metleucauge	+	+	S	?	+	−	?
Chrysometa	+	+	+	−	+	+	+
Homalometa	+	+	S	?	+	+	?
Nephila	−	+	S	+	+	−	N
Zygiella	+	+	S	−	+/−	+	?
Araneidae							
Argiope	−*	−	−	−	−	+/−	−
Araneus	−*	−	−	−	−	−	−
Micrathena	−*	−	−	−	−/+	−	−

† Numbers refer to paragraphs in text under Relationships. 2. Male palpal tibia long, cone-shaped (+), short, wider than long (−), with bulges (*); 3. Secondary eyes with canoe-shaped tapetum (+), with tapetum lost in at least posterior median eyes (L), with canoe-shaped tapetum reduced and moved laterad (−); 4. Chelicerae of male longer than those of female (+), same size (S), smaller than female (−); 6. Femoral-patellar joint of legs held straight out at rest (+), flexed (−); 7. Epigynum lost (L), flat (+), three dimensional (−); 8. Abdomen cuticle underlain with numerous white or silver pigment spots (+), with few white silver spots (−); 10. Web construction behavior tetragnathid (+), nephiline (N), araneid (−) (see Eberhard, 1982).

in hub construction. According to observations by Eberhard, the hub is left intact in some species of *Glenognatha* and *Tetragnatha*, while in *Meta* and *Metellina* the hub center is removed and a hole left in the middle. *Dolichognatha* and *Azilia*, like most araneids, replace the center after its removal. According to other literature, temperate *Tetragnatha* have an open hub (Kaston, 1948; Wiehle, 1963) like the metines observed by Eberhard. Hub construction is probably too variable to be useful, although it is widely quoted as a differentiating character.

11. Vollrath (in manuscript) observed that *Nephila*, *Zygiella*, *Meta*, and possibly *Tetragnatha* suppress regeneration of lost legs at the coxal joint, along with theridiids and linyphiids. *Araneus* and *Argiope* in contrast regenerate lost legs.

Unfortunately, in none of these behavioral differences is tetragnathid behavior clearly specialized. I plan to return to this problem when revising the remaining neotropical Tetragnathidae.

There are two controversial groups: *Nephila* and its relatives and *Zygiella*.

Gerhardt (1923, 1933) considers the *Nephila* palpus secondarily reduced. But the similarities in palpal anatomy of *Leucauge* and *Nephila*, the convoluted duct in the large tegulum (also present in *Azilia* but unusual in other spiders), the distal placement of the embolus, and the embolus wrapped in the conductor are probably synapomorphies. Additional similarities between species of the two genera are coloration and abdomen shape. The unusual bottle-brush setae on the legs of the American *Nephila clavipes* may be homologous to those found in some Indopacific *Leucauge* species, which Archer (1951) placed into *Opadometa*. However, the short, broad palpal tibia of the small *Nephila* males may reflect its araneid mating position.

Gerhardt (1923, 1933) comments on the similar, reduced palpi of *Gasteracantha* and *Micrathena*, but the palpi of these two genera resemble those of other Ara-

neinae (Levi, 1978, 1985). The palpus of *Nephila*, in contrast, is similar to that of *Leucauge*.

Homann (1952) was in error when he wrote that *Nephila*'s eyes are araneid (Homann, personal communication). They do not have the narrow canoe-shaped tapetum characteristic of Araneidae.

Nephila (Eberhard, 1982) and the related *Nephilengys* and *Herennia* differ in web-building behavior from both tetragnathids and araneids (Eberhard, 1982). The sticky spiral attachment point is located by extending the outside (relative to the spiral) leg IV backward and sidling it along from one point to the next, rather than moving it inward to the hub and then back out again. The order of radii placement differs from both araneids and tetragnathids: after one trip out from the hub, two radii are attached to two points on the frame; other spiders attach only one radius. The original hub is left intact, not bitten out or replaced. Nonsticky spirals are retained. All prey is attacked by biting and only sometimes wrapped afterwards. The first two behaviors (radii and hub) may be specialized, while the third and fourth are probably primitive (Eberhard, 1982).

Zygiella has an eye arrangement and tapetum structure similar to *Meta* (Levi, 1974), and a palpus with a similar cone-shaped tibia. The structure of the palpal organ is more complex, however, having a median apophysis and two sclerites (radix and stipes) at the base of the embolus. Apparently the median apophysis and some of these sclerites evolved independently several times (e.g., in Linyphiidae, Theridiidae) from metine-like ancestors. If the function of the median apophysis is to hook into the scape of the female epigynum, and only some *Zygiella* species (*Z. stroemi*, *Z. kochi*) have a scape, then the median apophysis might represent a vestige in the scapeless *Z. x-notata* and *Z. dispar*. What then is its evolutionary significance in the scapeless Theridiidae? The paracymbium of *Zygiella* is complex and free, more closely resembling that of Tetragnathidae than that usually found in Araneidae. Also, the coloration and the white spots and dark markings of the abdomen are characteristic of Tetragnathidae, not of Araneidae. [Several *Chrysometa* were originally described in *Zilla* (=*Zygiella*).] (The distal hematodocha in Levi, 1974, figs. 7, 30 is mislabeled. It is not homologous to the hematodocha, called "distal hematodocha," of *Eriophora* and *Araneus*, located between embolus and terminal apophysis.)

Gerhardt (1933) writes that the mating position of *Zygiella* resembles that of *Meta*. It also resembles that of some *Araneus* species (Blanke, 1983).

It is perhaps easier to split than to lump, to elevate genera to families if they have autapomorphies that are distinct, and to elevate species groups to genera. Forster (personal communication) considers *Leucauge* to be in a family by itself. Perhaps this is correct; at present I am unaware of supporting evidence. *Glenognatha*, with its anterior spiracle, might be considered another candidate for splitting off into its own family, although it is otherwise similar to the large-sized *Pachygnatha*. The advanced spiracle probably represents physiological adaptation to small size and resultant greater water loss.

Chrysometa Simon

Chrysometa Simon, 1895: 736. Type species *Chrysometa tenuipes* (Keyserling) by original designation.

Pseudometa F.P.-Cambridge, 1903: 444. Type species *Pseudometa flava* (O. P. Cambridge) by original designation (not *Pseudometa* Aurivillius, 1901, a beetle.) NEW SYNONYMY.

Capichameta Soares and Camargo, 1955: 578. New name for *Pseudometa* F.P.-Cambridge, preoccupied. NEW SYNONYMY.

Synonymy. Simon designated, as type for *Chrysometa*, *Tetragnatha tenuipes* Keyserling, but misidentified the species. The specimens that Simon examined and called *C. tenuipes* came from St. Vincent Island, Lesser Antilles and were actually a new species close to *C. tenuipes*, here called *C. eugeni* (Figs. 628–634). *Pseudometa flava* (Figs. 530–536) has genitalia

similar to those of *C. tenuipes* (Figs. 647–651), but the abdomen is differently shaped and colored.

Diagnosis. Chrysometa differs from the related *Metellina* by the genitalia: in males, by the presence of an apophysis on the cymbium (Figs. 17, 21) of the palpus; and by the presence of a more distinct terminal apophysis (A in Figs. 18–22), which is usually attached to the embolus. In females, the fertilization ducts of the epigynum are often more sclerotized than the connecting ducts (Figs. 577, 589, 594).

Chrysometa differs from the species of the "*Meta porteri*" group found in Chile by lacking the numerous teeth on the outside of the palpal cymbium of the male, and by lacking the projecting epigynum of the female. Also, *Chrysometa* species are smaller than species of the "*Meta porteri*" group.

Chrysometa has been confused with *Zygiella* and *Leucauge*. No native *Zygiella* species are known from the neotropics. *Chrysometa* males lack a median apophysis whereas *Zygiella* has one. The eye region of the carapace is narrower in *Chrysometa* (Figs. 1–4) than in *Leucauge*, and the palpal and epigynal anatomy differ. The color pattern of the underside of the abdomen in *Leucauge* is diverse, while it is almost always dusky to black with a longitudinal light line on each side in *Chrysometa* (Fig. 144).

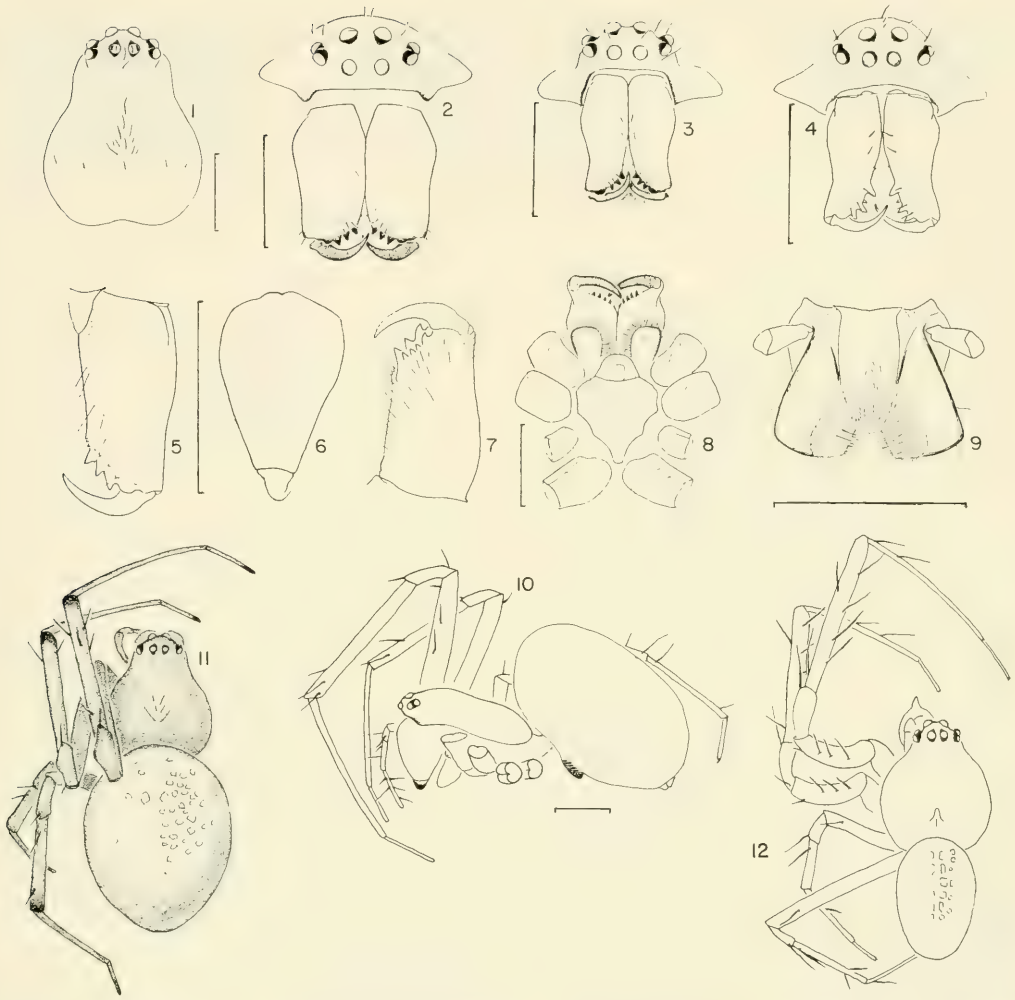
Chrysometa lacks the long trichobothria on the fourth femur characteristic of *Leucauge*. Some species of *Chrysometa* are superficially quite similar in appearance to the theridiid *Thwaitesia* (Levi, 1963).

Description. Coloration. Carapace orange with black eye rings. Often a characteristic brown patch covers the top of the head, but not its sides, coming to a point in the middle of the thorax. The patch may enclose paired light areas (Figs. 31, 82). Chelicerae are sometimes dark; sternum and labium are orange, occasionally dark brown to black, contrasting with the light coxae. The legs are orange, frequently with dark rings. The abdomen is covered by silver spots; there may be dark pigment anteriorly, or an irregular patch on each side on the shoulders and a posterior median band made of transverse black bars (Figs. 377, 393, 573). The venter of the abdomen in almost all species is dusky to black with a light longitudinal line of silver spots on each side (Figs. 144, 326, 339). In some species the line begins or ends in a larger silver patch, constricting the black area (Fig. 467).

Structure. The carapace is narrow in front, the thoracic depression indistinct (Figs. 1–4). In males the thoracic depression is only rarely distinct. The eyes are large, subequal in size; the secondary eyes have a canoe-shaped tapetum which may be narrowed in the posterior median eyes and situated toward the midline of the spider (unlike the narrowed tapetum of Araneidae which is situated laterally). The anterior median eyes are about their diameter apart, the same distance or slightly more from the laterals. The posterior median eyes are their diameter apart, one to two diameters from the laterals. The laterals on each side touch. The clypeus height equals about one anterior median eye diameter (Figs. 1–4, 10–12).

The chelicerae of all species have three strong teeth on the anterior margin, four small teeth or denticles on the posterior margin. The second denticle from the proximal end of the posterior margin may be smaller and may have moved anterior toward the midline (Figs. 5–7). The chelicerae also have some small tubercles bearing setae in front of the anterior three teeth and at the proximal end of the fang groove. The venom glands are small and barely extend beyond the chelicerae (in *C. alboguttata*). Males have the chelicerae longer than conspecific females, as is common in tetragnathids (Fig. 4). The first leg is longest, the third shortest, and the second only slightly longer than the fourth. Males have longer legs than females (Figs. 10–12).

The abdomen varies in shape among species; it is usually oval, widest at the middle or slightly anterior to the middle.



Figures 1–12. Morphology of *Chrysometa*. 1. Female carapace. 2. Female eye region and chelicerae. 3, 4. Male eye region and chelicerae. 5–7. Female chelicerae. 5. Anterior. 6. Lateral. 7. Posterior. 8. Female coxae, sternum and chelicerae. 9. Female endites and rostrum, anterior. 10, 11. Female. 10. Lateral. 11. Dorsal. 12. Male. 1–3, 8, 10–12. (*C. flava*). 4. (*C. cornuta*). 5–7, 9. (*C. alboguttata*).

Scale lines. 1.0 mm.

Some species have a spherical abdomen (Fig. 656); in others there are two anterior dorsal humps (Fig. 340); in those species having the abdomen all silver, the abdomen has a slight anterior median projection (Figs. 687, 688, 696, 707).

Unlike in *Tetragnatha* species, abdomen size varies little among adults. Males are slightly smaller than females.

Genitalia. The female epigynum may have a septum continuing into a posterior transverse bar. To the sides of the septum or bar are the openings (Fig. 14). Sometimes the epigynum is heavily sclerotized; it only rarely has a scape (Figs. 336, 343). The epigynum opens into connecting ducts leading to sclerotized seminal receptacles which often have sclerotized, perhaps secretory, lobed structures next to them. From the base of the seminal receptacles

originate sclerotized fertilization ducts (Figs. 576, 577, 588, 589). It is uncommon in spiders for these ducts to be sclerotized. The female duct system is quite unusual in its complexity. Although the sclerotized fertilization ducts are located ventrally, they are often surrounded by and seemingly imbedded in the connecting ducts. The connecting ducts are short in females conspecific with males having a short embolus. In many species the ventral side of the epigynum has a pair of smooth, thin-walled, spherical structures, apparently attached to the fertilization ducts as well as to the connecting ducts (Figs. 555, 562). They do not contain sperm, and their function is unknown. This spherical structure may have been overlooked in some species of which few specimens were available. The walls of the connecting ducts are frequently pleated, rarely sclerotized, always difficult to follow. Often they seem to follow the course of an Escher-like paradox.

The male palpal structure is also difficult to make out; it is most easily seen in males with a short, sclerotized embolus and conductor. The embolus is supported by a parallel structure originating from its base, the terminal apophysis (A in Figs. 18–22). Embolus and terminal apophysis are in turn supported by the conductor (C), a free sclerite that may be long. In those species having a long embolus and terminal apophysis, the structures are difficult to distinguish in an unexpanded palpus (Figs. 16, 17). When long, these two sclerites may originate from inside a cup-shaped tegulum (Figs. 18, 19). The cymbium always has an apophysis (Fig. 17); the paracymbium is a separate sclerite broadly attached to the cymbium.

Natural History. The web, where known (*C. poas, C. craigae*), is an orb with a signal line and a retreat. The retreat is commonly on a branch or on the base of a leaf (Plate 1). Between retreat and hub is a vacant sector. The web resembles that of *Zygiella*. At its type locality, *Chrysometa poas* does not have the vacant sector. According to Eberhard (personal communication, 1985), there are three recognizable types of web: one, the webs of *Chrysometa alboguttata* and *C. guttata* with a free sector and very round hub and bell-shaped retreat; two, *C. saladito* and *C. calima* with a retreat but usually not a free sector and a more oval hub (these species switch from *Tetragnatha*-like to *Araneus*-like sticky spiral localization behavior during the construction of each web); and three, *C. digua*, etc.-type with little if any retreat and with neither a free sector nor a distinctly oval hub. I suspect that the order of listing is from the most to the least derived web (Plate 1). The spiders do not extend their legs when resting (Plate 1).

The spiders are found in shaded forests, or, if above timberline, in paramos on steep, shaded slopes.

All specimens from northern Colombia lacked the silver spots. Is this due to the preserving fluid or to a genetic variation of the species of the area?

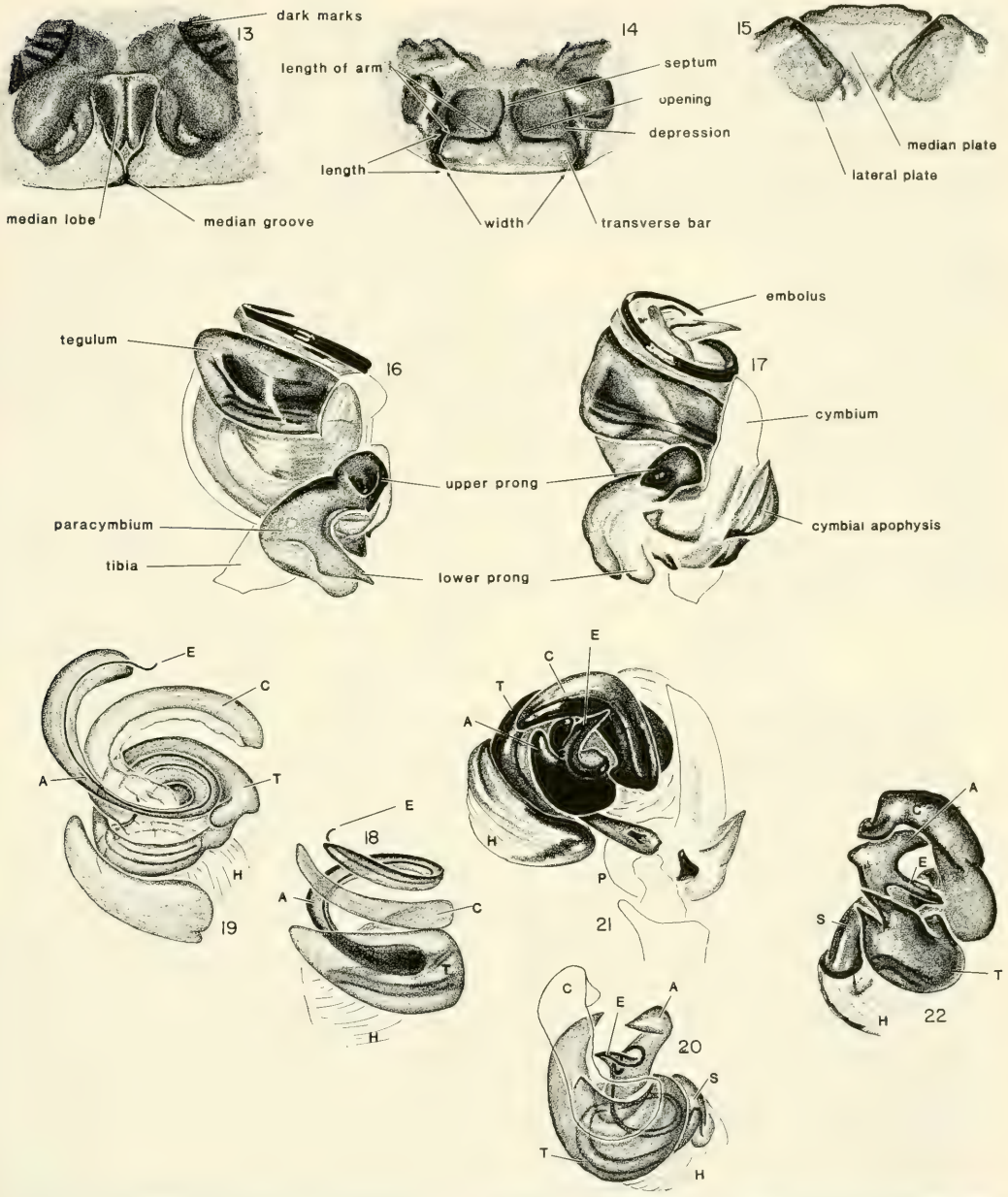
Distribution. Species are known from the mountains of Mexico to Bolivia and at lower elevations from Central America to Brazil (Map 1). While the distribution of species reflects popular collecting sites, many more species are expected from other ranges of the Andes (Maps 2–4).

Misplaced Species

Chrysometa species have been named in several genera: *Capichameta, Chrysometa, Meta, Pseudometa* and *Zilla*. Some have also been named in *Argyroepeira* or *Leucauge*. The following is the correct placement of those species which do not belong to *Chrysometa*. They are listed here in alphabetical order of the original combination. *Argyroepeira* and *Leucauge* species are not listed since most are correctly placed in *Leucauge* in the catalogs of Roewer (1942), Bonnet (1957), and Brignoli (1983).

Chrysometa T-notata Tullgren, 1905: 28, pl. 3, fig. 8, ♀. Female holotype from Argentina (NRS), examined, is *Larinia T-notata*. NEW COMBINATION.

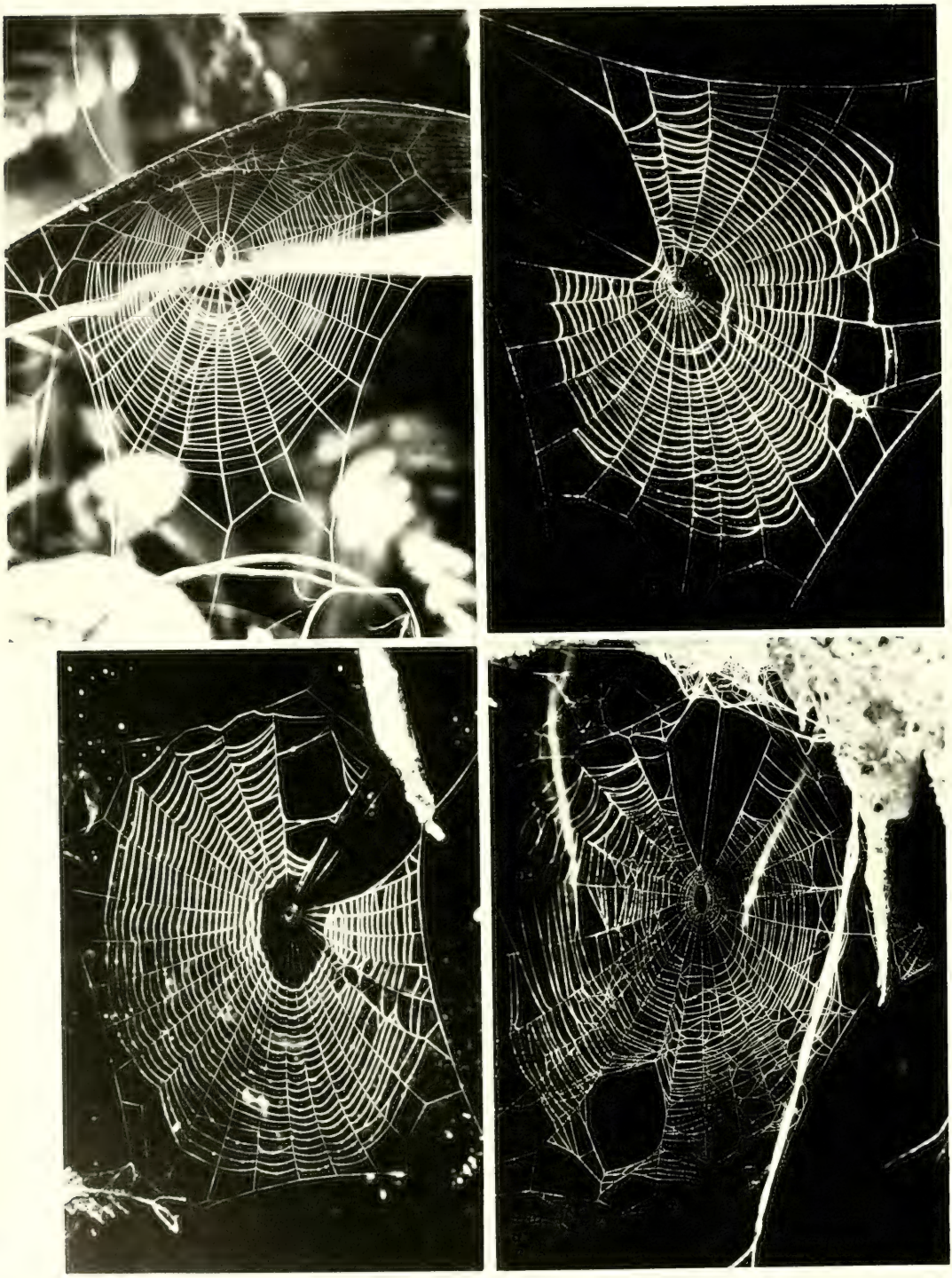
C. tristis Mello-Leitão, 1941: 153, fig. 49, ♀. Female



Figures 13–22. Genital morphology of *Chrysometa*. 13–15. Epigynum. 13, 14. Ventral. 15. Posterior. 16–22. Left male palpus. 16. Ventral. 17. Lateral. 18–22. Expanded. 13. (*C. minuta*). 14, 15. (*C. boraceia*). 16, 17. (*C. guttata*). 20, 22. (*C. troya*). 21. (*C. zelotypa*).

Scale lines. 0.1 mm.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; H, basal hematodocha; P, paracymbium; T, tegulum.



holotype from Argentina (MULP), examined, is *Dubiaranea tristis*. NEW COMBINATION in family Linyphiidae.

Epeira longipes Nicolet, 1849: 491. Specimens from Chile (MNHN), examined, belong to the *Meta porteri* group.

Linyphia branickii Taczanowski, 1873: 67. Female holotype from Guyana (PAN), examined; placed by Petrunkevitch, 1911 into *Chrysometa* is *Leucauge branicki*. NEW COMBINATION.

L. melanocephala Taczanowski, 1873: 70. Female holotype from Guyana (PAN), examined; placed by Keyserling (1893) in *Zilla* is *Mangora melanocephala*. NEW COMBINATION.

Meta adjuntaensis Petrunkevitch, 1930: 346, fig. 234, ♀. Female holotype from Adjuntas, Puerto Rico (PMY), lost, is *Araneus adjuntaensis*. NEW COMBINATION.

M. aurora Simon, 1901: 19. Female holotype from Patagonia (MNHN), examined, belongs to the *Meta porteri* group.

M. berlandi Caporiacco, 1954: 80, fig. 80, ♀. Female from French Guiana (MZUF), examined, is *Cyrtophora guyanensis* (Keyserling). NEW SYNONYMY.

M. blanda Bryant, 1945: 386, fig. 22, ♀. Female type from Hispaniola (MCZ), examined, is *Araneus blanda*. NEW COMBINATION.

M. brasilica Soares and Camargo, 1948: 380, figs. 37–39, ♀ ♂. Female holotype from Est. São Paulo, Brazil (MZSP), examined, is *Cyrtophora guyanensis* (Keyserling). NEW SYNONYMY.

M. bryantae Brignoli, 1983: 320. New name for *Meta blanda* Bryant (not *Meta blanda* C. L. Koch) is *Araneus blanda*. NEW COMBINATION.

M. chilensis Tullgren, 1902: 22, pl. 1, fig. 7, ♀. Female holotype from Chile (NRS), examined, belongs to the *Meta porteri* group.

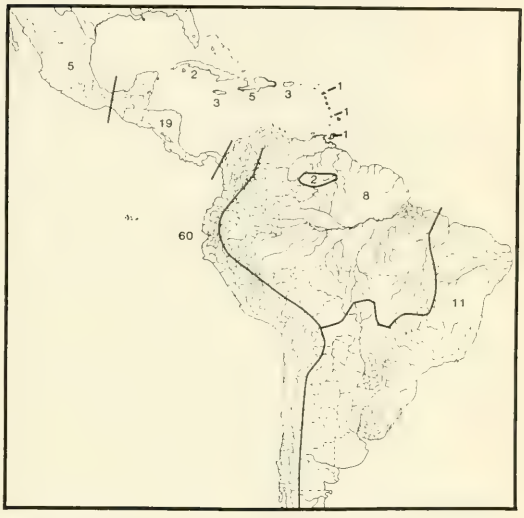
M. cordillera Tullgren, 1902: 23, pl. 2, fig. 3, ♀. Female holotype from Chile (NRS), examined, belongs to the *Meta porteri* group.

M. echinata Tullgren, 1902: 19, pl. 2, fig. 1, ♂. Male holotype from Chile (NRS), examined, belongs to the *Meta porteri* group.

M. espiritosantensis Soares and Camargo, 1955: 578, figs. 4, 5, ♂. Male holotype, lacking both palpi, from Est. Espírito Santo, Brazil (MZSP), examined, is *Cyrtophora guyanensis* (Keyserling). NEW SYNONYMY.

M. fuegiana Simon, 1902: 26. Female holotype from Tierra del Fuego (MNHN), examined, belongs to the *Meta porteri* group.

M. globosa O. P.-Cambridge, 1889: 2, pl. 1, fig. 5, ♀. Female holotype from Guatemala (BMNH), examined, is the type species of the genus *Mecynometa* Simon 1895 and is *Leucauge globosa*. NEW COMBINATION.



Map 1. Approximate number of species of *Chrysometa* known from different regions.

M. gravida (O. P.-Cambridge, 1899: 290) placed by Roewer (1942) in *Meta*, is *Metabus gravidus* O. P. Cambridge.

M. hotteiensis Bryant, 1945: 387, fig. 25, ♀. Female holotype from Hispaniola (MCZ), examined, is *Araneus hotteiensis*. NEW COMBINATION.

M. longimana Keyserling, 1881: 555, pl. 16, fig. 6, ♀. Female holotype from Peru (PAN), examined, placed by Petrunkevitch, 1911 in *Chrysometa*, is *Leucauge longimana*. NEW COMBINATION.

M. mariana Keyserling, 1881: 560, pl. 16, fig. 10, ♀. Female syntypes from Peru (BMNH), examined, are *Leucauge mariana*. NEW COMBINATION.

M. nigrohumeralis F. P.-Cambridge, 1898: 18, pl. 2, fig. 4, 5, ♀. Female holotype from Juan Fernandez Islands (BMNH), examined, belongs to the *Meta porteri* group.

M. patagiata Simon, 1901: 18. Female holotype from Chile (MNHN), examined, belongs to the *Meta porteri* group.

M. porteri Simon, 1900: 51. Female holotype from Chile (MNHN), examined, belongs to the *Meta porteri* group.

M. torta Tullgren, 1902: 21, pl. 2, fig. 2, ♂. Male

←

Plate 1. *Chrysometa* webs. Above left, *C. saladito*, sticky spiral area 11 cm wide. Above right, *C. zelotypa*, sticky spiral area 14 cm wide (from Costa Rica). Below left, *C. craigae*, sticky spiral area 16 cm wide. Below right, *C. palenque*, sticky spiral area 14 cm wide (photo above left W. Eberhard, others J. Coddington).

holotype from Chile (NRS), examined, belongs to the *Meta porteri* group.

M. speciosissima Keyserling, 1881: 557, pl. 16, fig. 8, ♀. Female holotype from Pumamarca, Peru (PAN), examined, is *Leucauge speciosissima*. NEW COMBINATION.

Zilla bösenbergi Keyserling, 1878: 575, pl. 14, figs. 4, 5, ♀. Female, male syntypes from Uruguay (ZIMH), examined, is *Zygiella x-notata*. NEW SYNONYMY.

Z. decolorata Keyserling, 1893: 306, pl. 15, fig. 226, ♀. Female holotype from Guatemala, but male specimen from Blumenau, Brazil (BMNH), examined, is a *Mangora*.

Z. guyanensis Keyserling, 1881: 554, pl. 16, fig. 5, ♂. Male holotype from Cayenne, French Guiana (PAN), examined, is *Cyrtophora guyanensis*. NEW COMBINATION.

Z. rogenhoferi Keyserling, 1878: 578, pl. 14, fig. 6, ♀. Female holotype from Brazil (NHMW), examined, is *Metazygia rogenhoferi*. NEW COMBINATION.

Lost types and unrecognizable names

Argyroepeira preciosissima Keyserling, 1893: 367, pl. 19, fig. 274, ♀. Female holotype from Guatemala (BMNH), lost. It had been placed into *Meta* by Petrunkevitch, 1911, but it is probably a small species of *Leucauge*.

A. voluptabilis Keyserling, 1893: 356, pl. 18, fig. 263, ♂. Male from Monte Verde, Est. Rio de Janeiro, Brazil (BMNH), lost. It had been placed into *Meta* by Petrunkevitch, 1911. It is probably a *Chrysometa*.

Meta albisparsa Mello-Leitão, 1944: 332. Male from Argentina (MULP), lost. The description is not recognizable.

M. longipes Keyserling, 1881: 274, pl. 11, fig. 4. Male and female syntypes from Pumamaria [sic Pumamarca, Dpto. Junín], Peru, lost (not in BMNH, PAN). This is probably a *Chrysometa*.

Zilla punctata Keyserling, 1893: 305, pl. 15, fig. 225, ♀. Female holotype from Nova Friburgo, Est. Rio de Janeiro, Brazil (BMNH), lost.

Key to Females

1. Epigynum in ventral view with an upside down T, a posterior transverse bar with a median anterior stalk or septum or attachment (Figs. 14, 521, 727) 2
– Epigynum otherwise 50
2 (1). Septum and transverse bar forming an anteriorly pointing triangle (Figs. 108, 642, 705) 3
– Septum and bar otherwise 5
3 (2). Epigynum as in Figure 705; Bolivia ..... *bolivia*
– Epigynum as in Figures 108, 642; Mexico, West Indies 4
4 (3). A large dark circle and dark patch on each side anterior of sculpturing of epigynum (Fig. 108); Cuba ..... *distincta*
– Two pairs of dark patches on each side anterior of sculpturing of epigynum (Fig. 642); Mexico ..... *puebla*
5 (2). Depressions of epigynum deep and large, septum very thin, only edge of transverse bar showing (Figs. 115, 727) 6
– Depressions, septum and bar otherwise 7
6 (5). Epigynum with transverse bar turning anteriorly on sides (Fig. 115); Central America ..... *nuboso*
– Epigynum and bar otherwise (Fig. 727); southern Brazil ..... *jordao*
7 (5). Septum as wide or wider than length of posterior transverse bar in ventral view (Figs. 225, 578) 8
– Septum narrower than length of posterior transverse bar (Fig. 14) 24
8 (7). Epigynum a triangular posteriorly extending bulge with paired depressions; depressions completely surrounded by rim (Fig. 225); Colombia ..... *carmelo*
– Epigynum otherwise 9
9 (8). Septum as long or longer than length of each arm of bar (Figs. 14, 517, 578) 10
– Septum shorter than length of each arm of transverse bar (Figs. 499, 609) 14
10 (9). Rim of septum continuing anterolaterally (Figs. 510, 517) 11
– Rim of septum otherwise 12
11 (10). In posterior view transverse bar bulging (Fig. 518); in ventral view dark parallel longitudinal marks anterior of sculpturing near midline (Fig. 517); Ecuador ..... *machala*
– In posterior view transverse bar relatively flat (Fig. 511); in ventral view a dark anterior mark on each side (Fig. 510); Costa Rica ..... *craigae*
12 (10). Stalk constricted posteriorly (Fig. 578); Colombia 13
– Stalk widest posteriorly (Fig. 637); Guyana to Amazon area ..... *flavicans*
13 (12). Anterior dark marks of epigynum paired, diagonal to transverse (Fig. 649) ..... *tenuipes*
– Dark marks as in Figure 578 ..... *fidelia*
14 (9). Arms of transverse bar swollen at lateral ends (Figs. 614, 676) 15
– Arms of transverse bar not swollen at ends (Figs. 499, 620) 16
15 (14). Septum bulging and constricted posteriorly (Fig. 614); Mexico ..... *chipinque*
– Septum otherwise (Fig. 676); Ecuador ..... *otavalo*

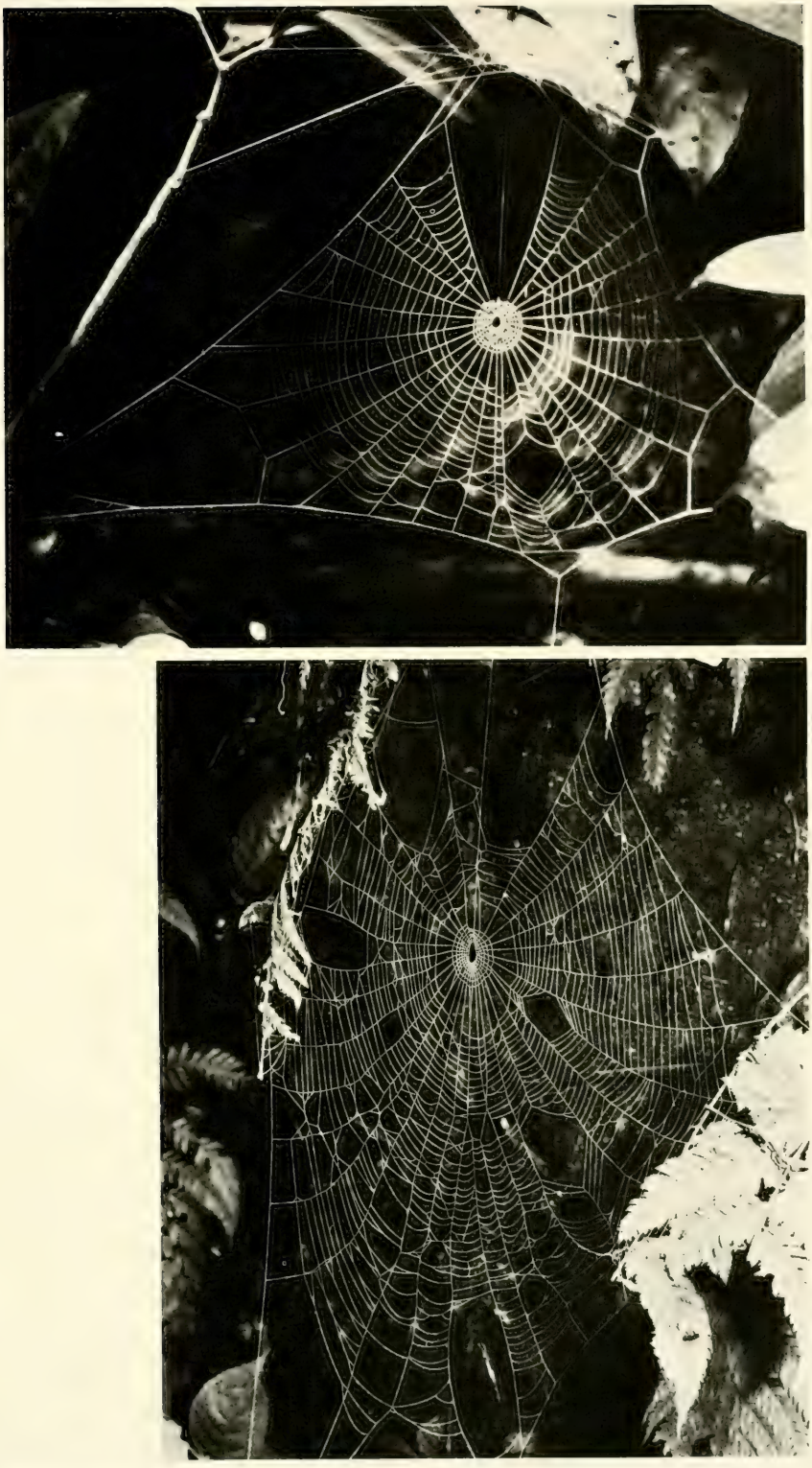


Plate 2. *Chrysometa* webs. Above, *C. guttata* (notice spider on leaf; sticky spiral area 18 cm wide). Below, *C. digua*, sticky spiral area 13 cm wide (photo W. Eberhard).

16 (14). Septum anteriorly with sclerotized lobes (Fig. 620); Rio Grande do Sul, Brazil ..... *cambara*
– Septum otherwise 17
17 (16). Septum wide, short, indistinct (Figs. 484, 499) 18
– Septum distinct (Figs. 254, 680) 19
18 (17). Septum wider (Fig. 499); Peru ..... *jelskii*
– Septum narrower (Fig. 484); Colombia ..... *rubromaculata*
19 (17). Septum and bar surrounded by semicircular lip as in Figure 254; Hispaniola ..... *conspersa*
– No such semicircular lip present 20
20 (19). Septum with anterior swelling (Fig. 680); Bolivia ..... *incachaca*
– Septum without anterior swelling 21
21 (20). Septum swollen posteriorly forming a median lobe (Fig. 693); Peru *opulenta*
– Septum without such posterior lobes 22
22 (21). Depression with diagonal openings (Fig. 685); Colombia ..... *calima*
– Depression otherwise 23
23 (22). Anterior of depression a border with a notch (Fig. 609); Honduras ..... *lancetilla*
– Anterior of depression a border curved (Fig. 630); Lesser Antilles ..... *eugeni*
24 (7). Sculptured area (area of septum, depression and transverse bar) distinctly wider than long (Figs. 489, 563, 665, 669) 31
– Sculptured area (area of septum, its lips, depression and transverse bar) square or longer than wide (Figs. 92, 549) 25
25 (24). Septum swollen anteriorly (Fig. 549); northern Colombia ..... *cebolleta*
– Septum otherwise (Fig. 92) 26
26 (25). Depression a longitudinal slit on each side of squarish septum (Fig. 92); Chile ..... *butamalal*
– Depression otherwise 27
27 (26). Depression bordered anteriorly and laterally (Figs. 153, 539) 28
– Depression not bordered anteriorly or laterally (Figs. 149, 525) 29
28 (27). Lateral and anterior border of depression continuous (Fig. 539); Colombia ..... *buenaventura*
– Lateral border below anterior border (Fig. 153); Bolivia ..... *chulumani*
29 (27). Transverse bar with anterior lobe on each side (Fig. 525); Colombia, Ecuador ..... *nigrovittata*
– Transverse bar without such lobe (Fig. 149, 470) 30
30 (29). Epigynum as in Figure 470; southeastern Brazil ..... *sumare*
– Epigynum as in Figure 149; northern Colombia ..... *sevillano*
31 (24). Lateral ends of transverse bar swollen (Figs. 563, 665, 669) 32
– Transverse bar otherwise 34
32 (31). Median plate in posterior view straight or convex anteriorly (Figs. 564, 670) 33
– Median plate in posterior view notched (Fig. 666); southern Mexico ..... *palenque*
33 (32). Width of bar about four times width of septum; no parallel dark marks anterior of sculpturing (Fig. 563); Mexico to Colombia ..... *alboguttata*
– Width of bar more than 5 times width of septum; parallel, longitudinal dark marks anterior of sculpturing (Fig. 669); Central America ..... *universitaria*
34 (31). Transverse bar with a lobe on each side of septum (Fig. 489); southern Mexico ..... *rincon*
– No such lobes present 35
35 (34). Septum with indistinct diagonal, rectangular depression on each side (Fig. 583); in posterior view (Fig. 584); Mexico, Central America ..... *brevipes*
– No such rectangular depressions; posterior view otherwise 36
36 (35). Width of transverse bar about five to six times its length and septum short (Fig. 660); Central America ..... *muerte*
– Transverse bar narrower 37
37 (36). Epigynum with indistinct comma-shaped depressions on each side of septum (Fig. 521); southern Brazil ..... *itaimba*
– Epigynum otherwise 38
38 (37). Septum and bar of about equal length, depressions indistinctly bordered (Fig. 177); Peru ..... *satulla*
– Septum, bar and depression otherwise 39
39 (38). Septum longer than bar with depression only indistinctly laterally bordered (Figs. 14, 570, 571); southern Brazil ..... *boraceia*
– Septum and depression otherwise 40
40 (39). Transverse bar rectangular, its width more than three times its length (Figs. 595, 596); Mexico, Central America ..... *poas*
– Epigynum otherwise 41
41 (40). Septum without lateral margins, only a break in slit around transverse bar (Figs. 474, 503, 556) 42
– Septum with lateral margins 44
42 (41). Distinct openings on anterior lateral margin of bar (Fig. 556); Colombia ..... *guttata*
– Epigynum otherwise 43

43 (42). Transverse bar oval with dark marks (Fig. 503); Central America ..... *decolorata*
– Transverse bar rectangular with dark marks (Fig. 474); Colombia ..... *niebla*
44 (41). Transverse bar with pair of dark triangular marks (Fig. 493); southeastern Brazil ..... *ludibunda*
– Transverse bar without dark marks 45
45 (44). Transverse bar an oval with dark marks (Fig. 479); Colombia ..... *buga*
– Transverse bar otherwise 46
46 (45). Depressions with diagonal anterior lip and dark marks as in Fig. 590; Colombia ..... *digua*
– Depressions and dark marks otherwise 47
47 (46). Depressions bordered anteriorly by curved lips and dark marks (Fig. 532); Mexico to Brazil ..... *flava*
– Epigynum otherwise 48
48 (47). Depressions bordered by curved margin of septum and bar, septum anteriorly pointed and dark marks (Fig. 654); Ecuador ..... *macuchi*
– Epigynum otherwise 49
49 (48). Depressions bordered by curved margin of septum and bar and with transverse dark marks (Fig. 544); Venezuela ..... *claudia*
– Septum and bar and dark streaks (Figs. 603, 604); Ecuador ..... *uaza*
50 (1). Epigynum with a sclerotized T within a transverse depression (Fig. 720) ..... *heredia*
– Epigynum otherwise 51
51 (50). Epigynum with a median scape-like structure, scape having raised border (Figs. 207, 343, 353) 52
– Epigynum otherwise 57
52 (51). Scape with anterior constriction (Figs. 336, 343) 53
– Scape without such constriction (Figs. 206, 357) 54
53 (52). Scape longer than wide (Fig. 343); Peru ..... *explorans*
– Scape wider than long (Fig. 336); Colombia ..... *bigibbosa*
54 (52). Scape in posterior view separating lateral plates (Fig. 207); Colombia ..... *eberhardi*
– In posterior view lateral plates covering scape (Figs. 349, 358); Ecuador 55
55 (54). Lateral borders of scape parallel (Fig. 357) ..... *cuenca*
– Lateral borders otherwise 56
56 (55). Scape set inside a sclerotized oval area which is three times as wide as long (Fig. 348); median groove of scape short (Fig. 348) ..... *macintyrei*
– Scape set inside a sclerotized triangular area (Fig. 353); median groove of scape extending anteriorly (Fig. 353) ..... *bolivari*
57 (51). Epigynum with a median (bordered) depression (Figs. 271, 276, 312), sometimes divided (Fig. 290) 58
– Epigynum without median (bordered) depression (Figs. 391, 396) 68
58 (57). With an anterior transverse ridge (sometimes reduced to a lobe) anterior of depression (Figs. 290, 312) 59
– No such median transverse ridge (Figs. 264, 415) 63
59 (58). Depression divided by a median sclerotized longitudinal septum (Fig. 290); Central America ..... *satura*
– Depression without median sclerotized division 60
60 (59). Lateral and posterolateral borders of depression continuous (Figs. 312, 314–316); Central America to Peru ..... *zelotypa*
– Lateral and posterolateral borders of depression forming angle (Figs. 271, 276, 283) 61
61 (60). Depression more than twice as wide as long (Fig. 271); Ecuador ..... *penai*
– Depression otherwise (Fig. 276, 283); Colombia 62
62 (61). Depression rectangular longer than wide (Fig. 283) ..... *kochalkai*
– Depression triangular, pointed posteriorly (Fig. 276) ..... *pilimbala*
63 (58). Anterior border of depression broken by a septum (Fig. 264, 415) 64
– Anterior border continuous (Figs. 423, 437) 65
64 (63). Septum a tongue as wide as depressions on each side (Fig. 264); Colombia ..... *huila*
– Septum a narrow ridge (Fig. 415); Ecuador ..... *troya*
65 (63). Depression bordered posteriorly (Figs. 115, 727) ..... *jordao, nuboso*
– Depression open posteriorly (Figs. 423, 437) 66
66 (65). Depression containing a median, indistinct septum and bordered posteriorly by a pair of lobes (Figs. 437, 438); Amazon ..... *minuta*
– Depression otherwise 67
67 (66). Depression touching posterior edge of epigynum (Fig. 423); Colombia ..... *purace*
– Oval depression its length distant from posterior edge of epigynum (Fig. 34); Bolivia ..... *yungas*
68 (57). Epigynum with a median longitudinal groove (Figs. 391, 404) 69

– Epigynum without a median longitudinal groove with at most a lobe at each side (Figs. 221, 713) 76

69 (68). Epigynum with an anterior projecting sclerite bearing a light colored area (Fig. 391); Ecuador ..... *browni*

– Epigynum otherwise 70

70 (69). Epigynum with an anterior lobe (Figs. 384, 396) or anterior transverse ridge (Figs. 295, 303) 72

– Epigynum without anterior structures (Figs. 368, 404); Ecuador 71

71 (70). Epigynum with longitudinal groove continuing laterally outlining a pair of lobes (Fig. 404) ..... *allija*

– Epigynum otherwise (Fig. 368) ..... *minza*

72 (70). Epigynum with a broad anterior lobe (Figs. 384, 396); Ecuador 73

– Epigynum with an anterior transverse bridge 74

73 (72). Epigynum with a depression on each side (Fig. 384) ..... *chica*

– Epigynum otherwise (Fig. 396) ..... *luisi*

74 (72). A pair of bordered depressions posterior to transverse ridge (Figs. 295, 303) 75

– No such depression posterior to ridge (Fig. 307); Colombia ..... *ecarup*

75 (74). Area of ridge and depressions its width distant from posterior edge of epigynum (Fig. 295); Central America ..... *bella*

– Area of ridge and depression less than its width distant from posterior edge of epigynum (Fig. 303); Ecuador ..... *pichincha*

76 (68). Epigynum in ventral view without sculpturing (sculpturing, if present, on posterior face of epigynum) (Figs. 222, 714) 77

– Epigynum in ventral view with a median septum or lobe or median transverse or longitudinal structure 85

77 (76). Posterior view of epigynum with a pair of depressions (Fig. 222); Colombia ..... *cali*

– Posterior view otherwise 78

78 (77). Posterior view with distinct sculpturing (Figs. 26, 30, 714) 79

– Posterior view otherwise 81

79 (78). In posterior view a median septum and transverse bar (Fig. 714); Central America ..... *alajuela*

– Posterior view otherwise (Figs. 26, 30); Jamaica 80

80 (79). Epigynum in ventral view with a wide median posterior lobe (Fig. 25); in posterior view with pattern of grooves and ridges (Fig. 26) ..... *pecki*

– Epigynum with an anterior transverse bridge having posterior notches (Fig. 29); in posterior view with three dorsoventral ridges, two grooves (Fig. 30) ..... *fuscolimbata*

81 (78). Epigynum with median posterior lobe (Figs. 181, 194) 82

– Epigynum otherwise (Figs. 39, 43) 83

82 (81). Epigynum with 3 equal sized lobes (Fig. 181); Peru ..... *lepida*

– Epigynum with median lobe largest and transverse dark marks (Fig. 194); Colombia ..... *saladito*

83 (81). A pair of small sclerites extending beyond the posterior margin of epigynum (Fig. 39); Venezuela ..... *duida*

– Epigynum without such sclerites but with median light area 84

84 (83). A dark sclerotized patch to side of median light area of venter of epigynum (Fig. 43); Hispaniola ..... *cornuta*

– No such dark sclerotized areas (Fig. 49); widespread ..... *saramacca*

85 (76). Epigynum with median septum, lobe or pairs of depressions in ventral view, lobe lacking an anterior transverse border (Fig. 404) or epigynum with a pair of transverse slits (Fig. 243) 86

– Epigynum with median longitudinal or transverse ridge having a transverse anterior border (Figs. 13, 217, 375) 111

86 (85). Epigynum framed by raised lobes on each side (Fig. 404); Ecuador ..... *ura*

– Epigynum with one median lobe or pairs of transverse slits (Figs. 243, 249) 87

87 (86). Epigynum with pairs of transverse slits (Figs. 243, 249) 88

– Epigynum otherwise 90

88 (87). Epigynum with median area extending posteriorly as a triangular sclerite (Fig. 259); Colombia ..... *magdalena*

– Epigynum with posterior border straight 89

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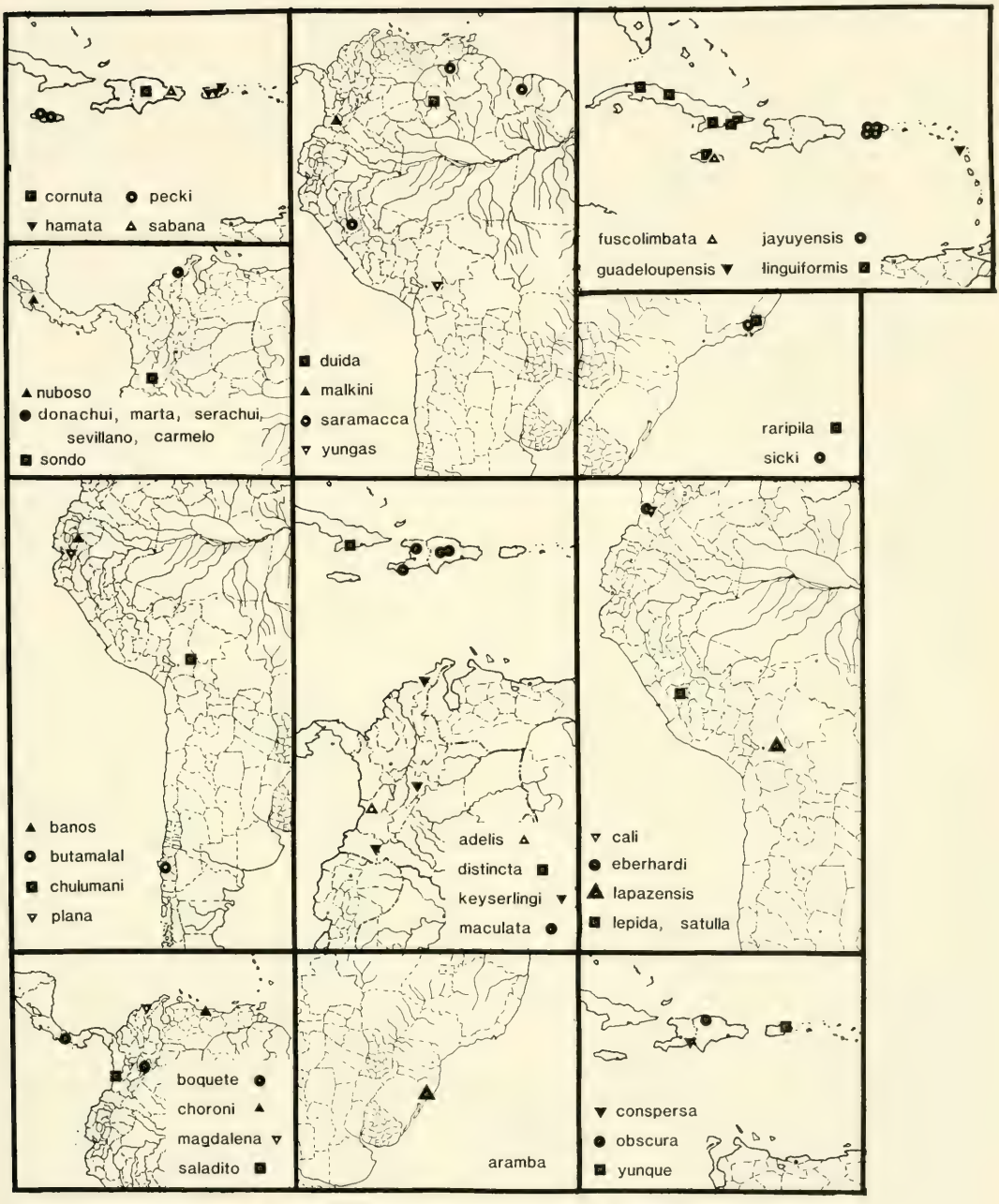
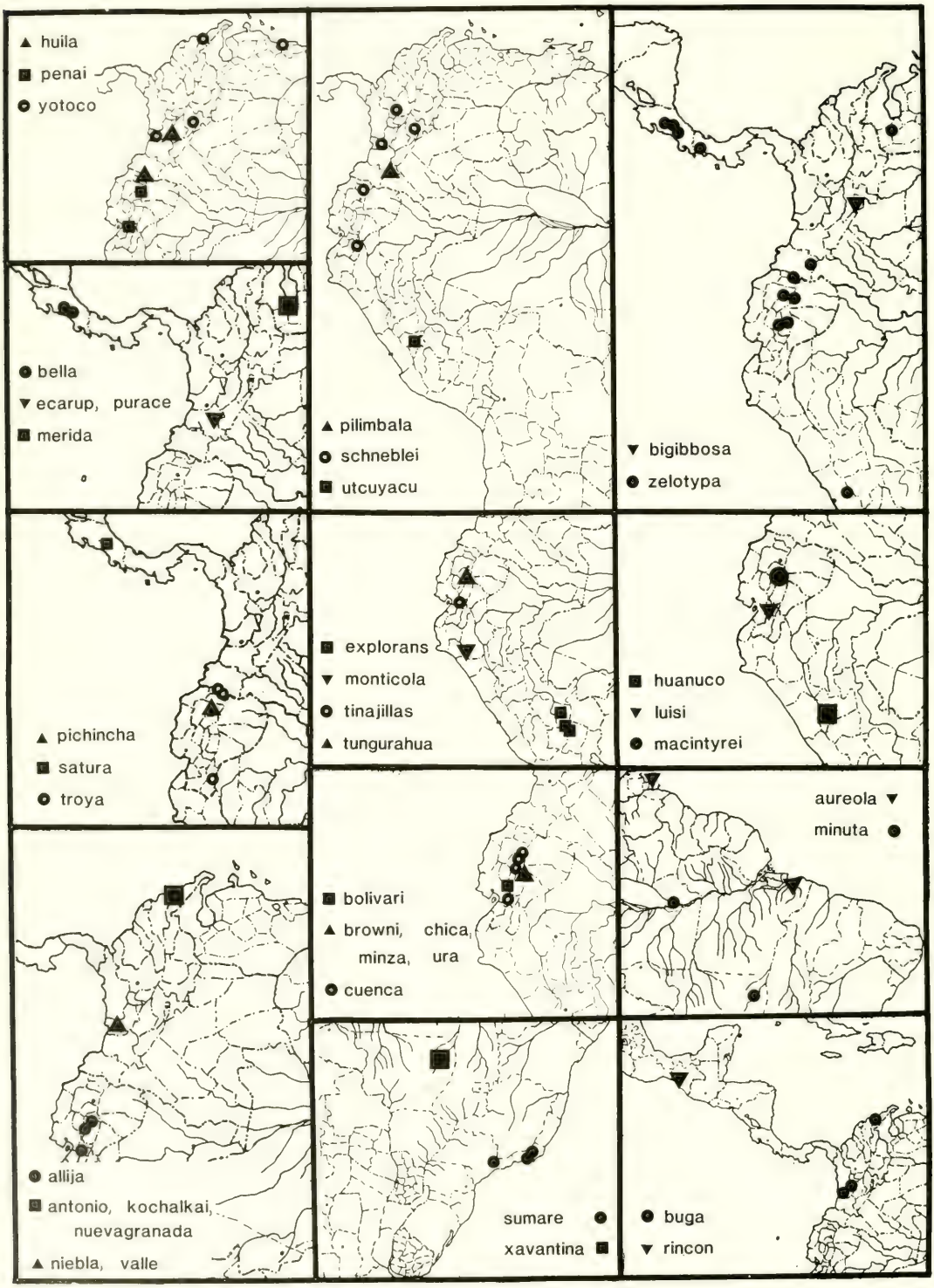
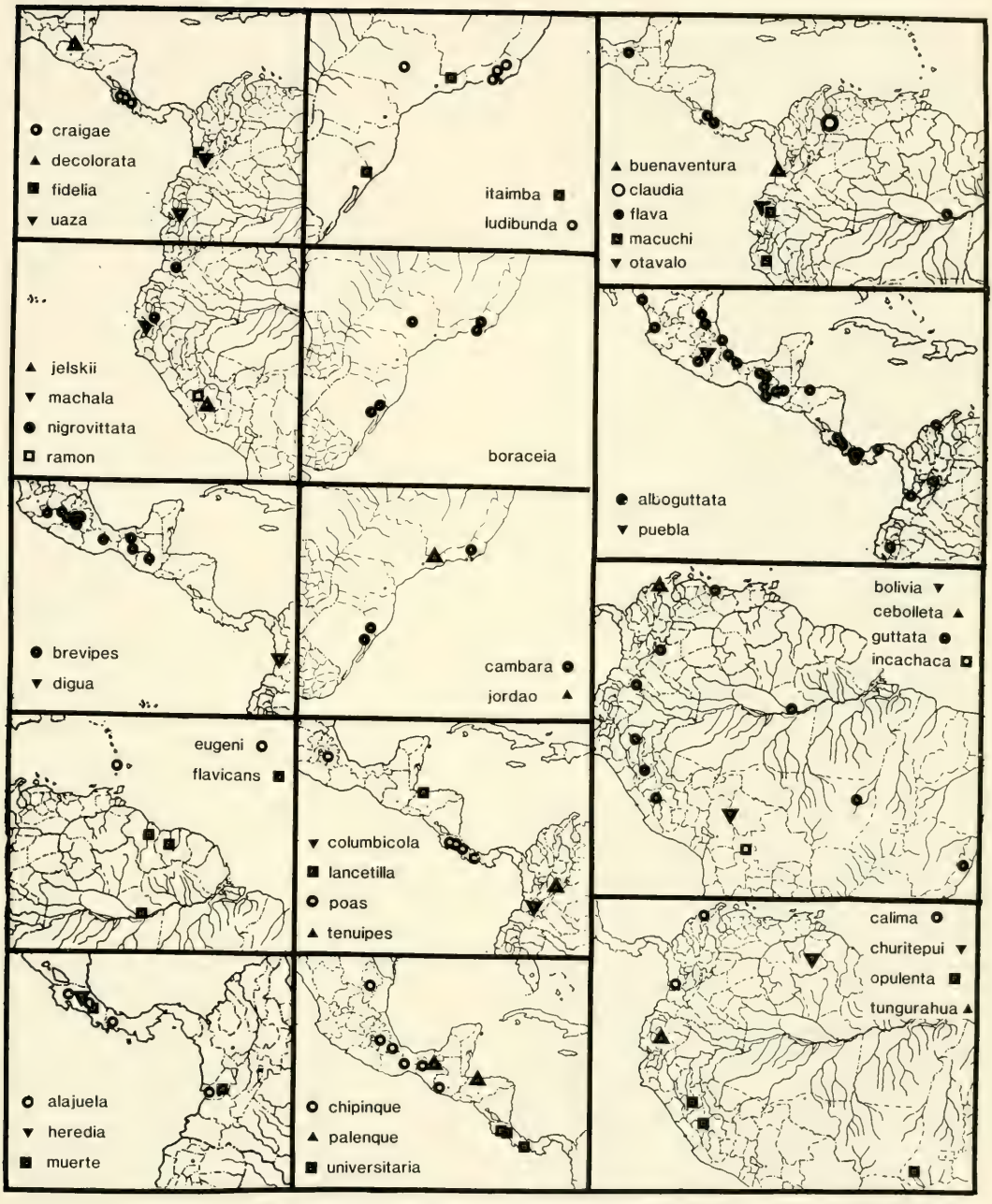
16(3). Palpal tibia more than one and a half times length of palpal cymbium (Figs. 125, 126); Colombia ..... *keyserlingi*



Map 2. Distribution of *Chrysometa* species.



Map 3. Distribution of *Chrysometa* species.



Map 4. Distribution of *Chrysometa* species.

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Chrysometa pecki new species
Figures 23–26; Map 2

Holotype. Female holotype with three female paratypes from Drip Cave, 2.5 km SSE of Stewart Town, Trelawny Parish, Jamaica, 2 April 1968 (S. Peck, A. Fiske, AMNH). The species is named after the collector.

Description. Female. Carapace orange, head black except on sides, with black area narrowing to a point on thoracic depression; chelicerae dark brown. Sternum yellow, sides black; legs orange with contrasting black rings. Dorsum of abdomen black with spots left free of pigment; sides black; venter black with central light area and longitudinal light lines on each side. Anterior median eyes very large. Secondary eyes equal to 0.7 diameters of anterior median eyes. Anterior median eyes 0.3 diameters apart, 0.4 from laterals; posterior median eyes 0.4 diameters apart, their diameter from laterals. Clypeus height equal to 0.3 diameters of anterior median eye. Abdomen subspherical. Total length, 6.6 mm. Carapace, 3.0 mm long, 2.3 mm wide. First femur, 3.5 mm; patella and tibia, 4.5 mm; metatarsus, 3.1 mm; tarsus, 1.2 mm. Second patella and tibia, 3.6 mm; third, 1.7 mm; fourth, 2.7 mm.

Variation. Individual from Hardwar Gap is lighter, with smaller black dorsal spots than holotype.

Diagnosis. The shape of epigynum, its smooth venter, and sculptured posterior (Figs. 25, 26) easily separate this species from *C. fuscolimbata* and others.

Paratypes. JAMAICA Hardwar Gap, Jan. 1966, ♀ (R. Kern, AMNH).

Chrysometa fuscolimbata (Archer), new combination
Figures 27–31; Map 2

Metargyra fuscolimbata Archer, 1958: 5, fig. 10. Female holotype from Hardwar Gap, 1,600 m, Port-

land Parish, Jamaica (AMNH), examined. Brignoli, 1983: 230.

Description. Female. Carapace yellow with brown marks (Fig. 31); chelicerae, labium, endites orange-brown; sternum orange, sides darker brown. Legs yellow, with contrasting brown rings. Dorsum of abdomen with pattern of black spots on brown and only few widely scattered silver spots (Fig. 31); venter with trapezoidal light mark, narrower in front than behind, containing silver spots surrounded by black patches. Secondary eyes equal to 0.7 diameters of anterior medians. Anterior median eyes 0.6 diameters apart, 0.7 diameters from laterals. Posterior median eyes 0.7 diameters apart, 1.4 diameters from laterals. Clypeus height equal to 0.4 diameters of anterior median eyes. Abdomen subspherical. Total length, 7.5 mm. Carapace, 3.4 mm long, 2.5 mm wide. First femur, 4.3 mm; patella and tibia, 5.2 mm; metatarsus, 3.9 mm; tarsus, 1.5 mm. Second patella and tibia, 4.0 mm; third, 1.9 mm; fourth, 3.1 mm.

Diagnosis. The wide transverse bar of the epigynum and paired median posterior notches (Fig. 29), and two parallel grooves in posterior view (Fig. 30) separate this species from *C. pecki.*

Record. JAMAICA Main Range, Blue Mountains, 1,600–2,300 m, 17–19 Aug. 1934, ♀ (P. J. Darlington, MCZ).

Chrysometa yungas new species
Figures 32–36; Map 2

Holotype. Female holotype and immature male paratype from Chulumani, 1,700 m, Yungas, Dpto. La Paz, Bolivia, 17–25 Dec. 1955 (L. Peña, IRSNB). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange-white with dusky patch in center, black between anterior median eyes; sternum dark brown; legs orange. Dorsum of abdomen with tiny silver spots about their diameter apart; venter with transverse black mark, black on sides and around spinnerets (Fig. 36). Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, their diameter from laterals. Posterior median eyes 1.5 diameters apart, slightly more than their diameter from laterals. Legs long. Abdomen oval. Total length, 4.2 mm. Carapace, 1.6 mm long, 1.4 mm wide. First femur, 6.3 mm; patella and tibia, 5.7 mm; metatarsus, 6.4 mm; tarsus, 1.1 mm. Second patella and tibia, 2.9 mm; third, 1.2 mm; fourth, 1.8 mm.

Diagnosis. This species is distinguished from all others by having a gap on the posterior side of the transverse oval depression in ventral view of the epigynum (Fig. 34).

Chrysometa duida new species
Figures 37–40; Map 2

Holotype. Female from Cerro Duida, savanna hill, Est. Amazonas, Venezuela (G. Tate, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange, dusky on margin of thorax; sternum black grading to orange in center; legs orange with indistinct dusky rings. Dorsum of abdomen with large silver spots, black patches on each shoulder grading into posterior band of black transverse marks. Venter with square median black patch; no distinct light lines. Anterior lateral eyes,

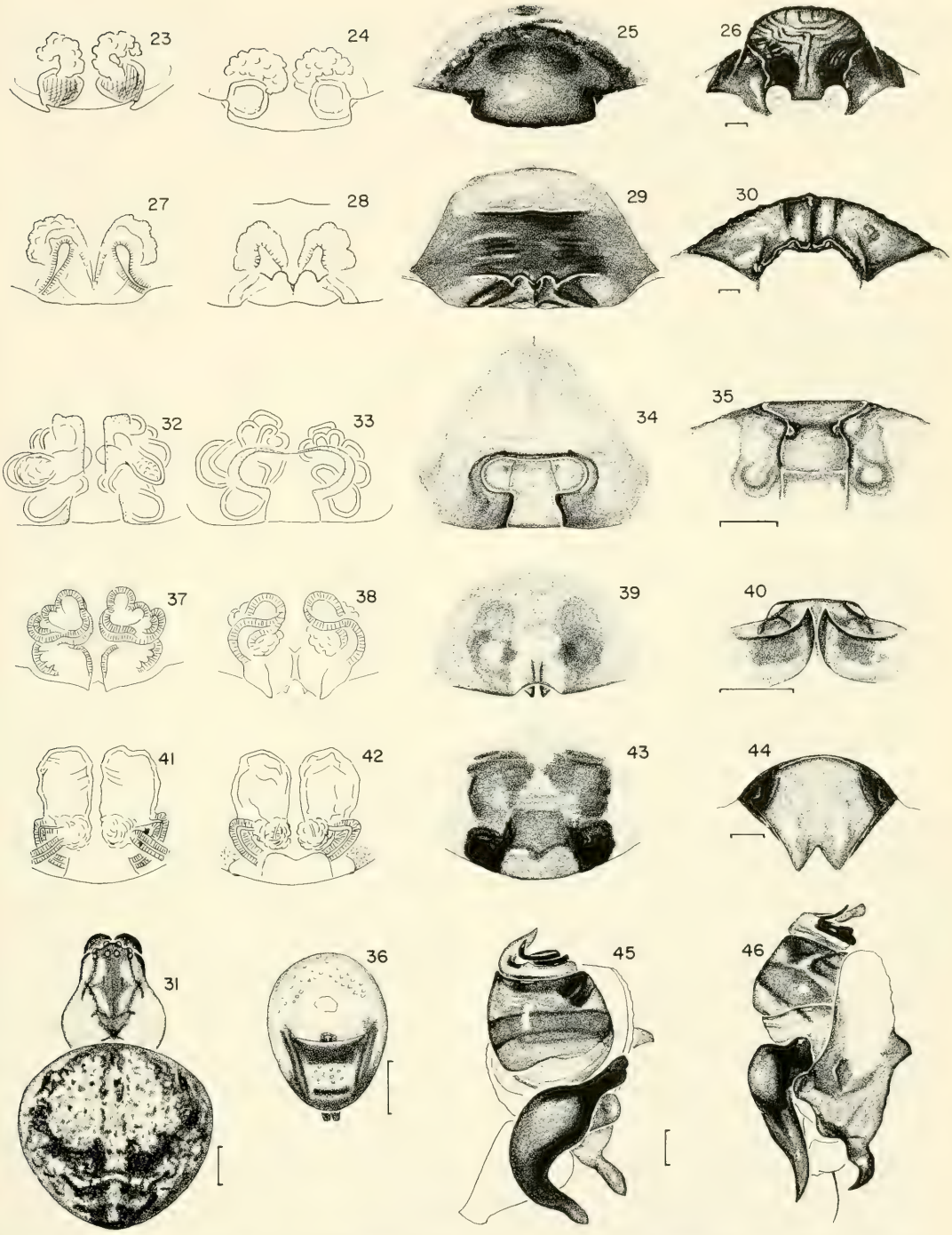
→

Figures 23–26. *Chrysometa pecki* n. sp., epigynum. 23. Dorsal, cleared. 24. Ventral, cleared. 25. Ventral. 26. Posterior.

Figures 27–31. *C. fuscolimbata* (Archer). 27–31. Epigynum. 27. Dorsal, cleared. 28. Ventral, cleared. 29. Ventral. 30. Posterior. 31. Female.

Figures 32–36. *C. yungas* n. sp. 32–35. Epigynum. 32. Dorsal, cleared. 33. Ventral, cleared. 34. Ventral. 35. Posterior. 36. Abdomen, ventral.

Figures 37–40. *C. duida* n. sp., epigynum. 37. Dorsal, cleared. 38. Ventral, cleared. 39. Ventral. 40. Posterior.



Figures 41–46. *C. cornuta* (Bryant). 41–44. Epigynum. 41. Dorsal, cleared. 42. Ventral, cleared. 43. Ventral. 44. Posterior. 45, 46. Male left palpus. 45. Ventral. 46. Lateral.

Scale lines. 0.1 mm, except Figures 31, 36, 1.0 mm.

posterior median eyes equal to 1.3 diameters of anterior medians; posterior lateral eyes 1.2 diameters of anterior median eyes. Anterior median eyes slightly less than their diameter apart, their diameter from laterals. Posterior median eyes slightly less than their diameter apart, same distance from laterals. Abdomen oval, spherical anterior half, pointed posteriorly. Total length, 3.0 mm. Carapace, 1.2 mm long, 1.0 mm wide. First femur, 1.7 mm; patella and tibia, 1.9 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm. Second patella and tibia, 1.3 mm; third, 0.7 mm; fourth, 1.0 mm.

Diagnosis. The venter of the epigynum, showing only a pair of posterior points (Fig. 39), and the curved, pointed lateral lobes in posterior view (Fig. 40) separate this species from others.

Chrysometa cornuta (Bryant), new combination
Figures 41–46; Map 2

Pseudometa cornuta Bryant, 1945: 392, figs. 26–28, ♀, ♂. Male holotype, female paratype from Loma Vieja, Cordillera Central, south of Constanza, 6,000′ [2,000 m], Dominican Republic (MCZ), examined.
Capichameta cornuta:—Brignoli, 1983: 227.

Description. Female. Carapace, sternum orange-yellow. Legs orange-yellow, ends of articles brown. Abdomen orange-yellow, without marks. Eyes subequal in size. Anterior median eyes 0.8 diameters apart, their diameter from laterals. Posterior median eyes slightly more than their diameter apart, the same distance from laterals. Total length, 4.5 mm. Carapace, 1.6 mm long, 1.2 mm wide. First femur, 2.2 mm; patella and tibia, 2.7 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 1.9 mm; third, 0.9 mm; fourth, 1.4 mm.

Male. Carapace with gray chevron on thorax, otherwise colored like female. Eyes subequal in size. Anterior median eyes their diameter apart, 1.3 diameters from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Abdomen suboval. Total length, 3.4 mm. Carapace, 1.6 mm long, 1.2 mm wide. First femur, 2.7 mm; patella and tibia, 3.2 mm; metatarsus, 2.9 mm; tarsus, 1.1 mm. Second patella and tibia, 2.2 mm; third, 0.9 mm; fourth, 1.4 mm.

Diagnosis. The epigynum, unlike that of *C. saramacca*, has a dark patch on each side of the light field (Fig. 43). The male differs from others in having the distinct paracymbium swollen at the middle (Figs. 45, 46).

Chrysometa saramacca new species
Figures 47–51; Map 2

Holotype. Female holotype from Voltzberg-Raleighvallen Nature Reserve, Saramacca Prov., Surinam, [04°32′N, 56°32′W], Feb. 1982 (D. Smith Trail, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow with black marks (Fig. 51); chelicerae yellow with basal black spot. Endites black proximally, with yellow sides; sternum black with five yellow patches anteriorly. Legs yellow, with contrasting narrow black rings. Dorsum of abdomen white with indistinct black marks anteriorly; venter with square black area, with longitudinal white line on each side, black patch on each side of epigynum and black ring around spinnerets. Carapace narrow in front. Secondary eyes equal to 0.4 diameters of anterior medians. Anterior median eyes almost touching, 0.3 diameters from laterals. Posterior median eyes 1.2 diameters apart, same distance from laterals. Abdomen oval. Total 4.4 mm. Carapace, 1.7 mm long, 1.2 mm wide. First femur, 2.3 mm; patella and tibia, 2.5 mm; metatarsus, 1.7 mm; tarsus, 0.9 mm. Second patella and tibia, 2.1 mm; third, 1.0 mm; fourth, 1.5 mm.

Variation. Total length varied from 3.0 to 4.4 mm among specimens from the type locality.

Diagnosis. The unique narrow head with large anterior median eyes raises a question whether this species is a *Chry-*

someta. It resembles species of *Dolichognatha* but, unlike *Dolichognatha*, has the posterior median eyes separated and lacks tubercles on the abdomen. It differs from *C. cornuta* by lacking a dark patch on each side of the light field of the epigynum (Fig. 49).

Natural History, Distribution. Low forest, Venezuela, Surinam, Amazonian Peru (Map 2).

Paratypes. VENEZUELA *Est. Bolívar:* 38 km E Ciudad Bolívar, 19 March 1982, ♀ (G. F., J. F. Hevel, USNM). PERU *Dpto. Huanuco:* Monson Vall., Tingo María, 26 Oct. 1954, ♀ (E. S. Ross, E. I. Schlinger, CAS).

Chrysometa hamata (Bryant) new combination
Figures 52–58; Map 2

Pseudometa hamata Bryant, 1942: 3, figs. 6, 8, 9, ♀, ♂. Male holotype, 3 female, one immature paratypes from El Yunque, 3,000 ft. [1,000 m], Puerto Rico (MCZ), examined.
Capichameta hamata:—Brignoli, 1983: 227.

Note. Bryant's (1942) figure 8 is upside down.

Description. Female. Carapace orange-yellow, head darker, with dusky patch in thoracic region. Chelicerae dark. Sternum light orange-yellow. Legs with dark rings. Dorsum of abdomen with indistinct pattern (Fig. 56); venter with dark band between epigynum and spinnerets, bordered on each side by a white line. Anterior lateral eyes 0.8 diameters of anterior medians; posterior median eyes 0.8 diameters; posterior lateral eyes 0.6 diameters of anterior medians. Anterior median eyes 0.5 diameters apart, 0.7 from laterals; posterior median eyes 0.5 diameters apart, their diameter from laterals. Abdomen subspherical (Fig. 56). Total length 6.0 mm. Carapace, 2.3 mm long, 1.9 mm wide. First femur, 2.9 mm; patella and tibia, 3.7 mm; metatarsus, 2.4 mm; tarsus, 1.1 mm. Second patella and tibia, 2.7 mm; third, 1.4 mm; fourth, 2.2 mm.

Male. Coloration, eyes like female. Anterior median eyes 0.5 diameters apart, 0.5 diameters from laterals. Posterior median eyes 0.5 diameters apart, their diameter from laterals. Total length, 4.3 mm. Carapace, 2.2 mm long, 1.8 mm wide. First femur, 3.8 mm; patella and tibia, 4.8 mm; metatarsus, 3.9 mm; tarsus, 1.2 mm. Second patella and tibia, 3.7 mm; third, 1.4 mm; fourth, 2.2 mm.

Variation. Females vary in total length from 3.5 to 6.0 mm, males from 3.1 to 4.3 mm.

Diagnosis. The female differs from other species by having a median lobe bearing a keel in ventral view of the epigynum (Fig. 54). The male can be separated from *C. cornuta* by the smaller sized, more "horizontally" placed paracymbium (Figs. 57, 58).

Natural History, Distribution. Found in intermediate elevation forest in Puerto Rico (Map 2).

Records. PUERTO RICO Adjuntas, June 1915, ♀ (A. Petrunkevitch, AMNH); El Yunque Nat'l. For., 4 Nov. 1971, ♀ (J. Carico, JC); Luquillo For., Municipio de Naguabo, 30 Aug. 1980, 3♀, ♂ (J. Coddington, MCZ).

Chrysometa sicki new species
Figures 59–62; Map 2

Holotype. Female holotype with two juvenile paratypes from Teresópolis, 1,000 m, Est. Rio de Janeiro, Brazil, bamboo undergrowth, March 1946 (H. Sick, AMNH). This species is named after the collector.

Description. Female. Carapace, legs yellow; sternum yellow, dusky posteriorly. Dorsum of abdomen with white pigment spots, posteriorly with transverse dusky marks; venter with gray patch between epigynum and spinnerets. Lateral eyes equal to 1.2 diameters of anterior medians; posterior median eyes equal to 1.4 diameters of anterior median eyes. Anterior median eyes slightly less than their diameter apart, their diameter from laterals. Posterior median eyes 0.6 diameters apart, 0.8 diameters from laterals. Abdomen oval. Total length, 2.8 mm. Cara-

pace, 1.4 mm long, 0.9 mm wide. First femur, 1.8 mm; patella and tibia, 2.0 mm; metatarsus, 1.6 mm; tarsus, 0.8 mm. Second patella and tibia, 1.6 mm; third, 0.8 mm; fourth, 1.2 mm.

Note. This small specimen may be the female of *Chrysometa voluptabilis* (Keyserling).

Diagnosis. This species is smaller than *C. malkini*, has a secondary posterior lobe on each side of the median septum of the epigynum, and lacks a dark sclerotized patch on each side of the median septum (Fig. 61).

Chrysometa malkini new species
Figures 63–66; Map 2

Holotype. Female from Paramo Puracé, 15 km E of Puracé, 3,000 m, Dept. Cauca, Colombia, beating foliage, 20 Oct. 1968 (B. Malkin, AMNH). The species is named after the collector.

Description. Female. Carapace orange with symmetrical dark reticulations and light spot above thoracic depression; sternum dark brown; legs yellow-orange, indistinctly ringed. Dorsum of abdomen with large silver spots absent in midline, black marks on shoulders; posteriorly with transverse bars forming a median black band. Venter dusky with a fine line of silver spots on each side. Lateral eyes equal to 1.5 diameters of anterior medians; posterior medians equal to 1.6 diameters of anterior median eyes. Anterior median eyes 1.3 diameters apart, two diameters from laterals. Posterior median eyes slightly less than their diameter apart, 1.2 diameters from laterals. Abdomen subspherical, slighty longer than wide, with shoulder humps. Total length, 4.2 mm. Carapace, 1.6 mm long, 1.2 mm wide. First femur, 2.3 mm; patella and tibia, 2.7 mm; metatarsus, 2.3 mm; tarsus, 0.9 mm. Second patella and tibia, 1.7 mm; third, 0.9 mm; fourth, 1.4 mm.

Diagnosis. Chrysometa malkini is larger than *C. sicki* and has a dark sclerotized patch on each side of the median septum (Fig. 65) of the epigynum.

Chrysometa sabana new species
Figures 67–70; Map 2

Holotype. Female holotype with one female paratype from forest between Hato Mayor and Sabana de la Mar, Dominican Republic, 20 July 1935 (W. G. Hassler, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum orange; legs orange with black spots. Dorsum of abdomen with white pigment spots and black spots, posterior half with longitudinal dark band widest in front; venter black with longitudinal line of white spots on each side, and transverse white line in front of spinnerets. Eyes subequal in size. Anterior median eyes 0.6 diameters apart, their diameter from laterals. Posterior median eyes 0.5 diameters apart, their diameter from laterals. Abdomen subspherical.Total length, 6.0 mm. Carapace, 2.9 mm long, 2.1 mm wide. First femur, 3.4 mm; patella and tibia, 4.2 mm; metatarsus, 3.2 mm; tarsus, 1.1 mm. Second patella and tibia, 3.2 mm; third, 1.7 mm; foruth, 2.5 mm.

Diagnosis. The median septum of the epigynum is round and, unlike that of *C. keyserlingi*, lacks an anterior lip (Fig. 69). In posterior view the septum has a constriction dorsally (Fig. 70).

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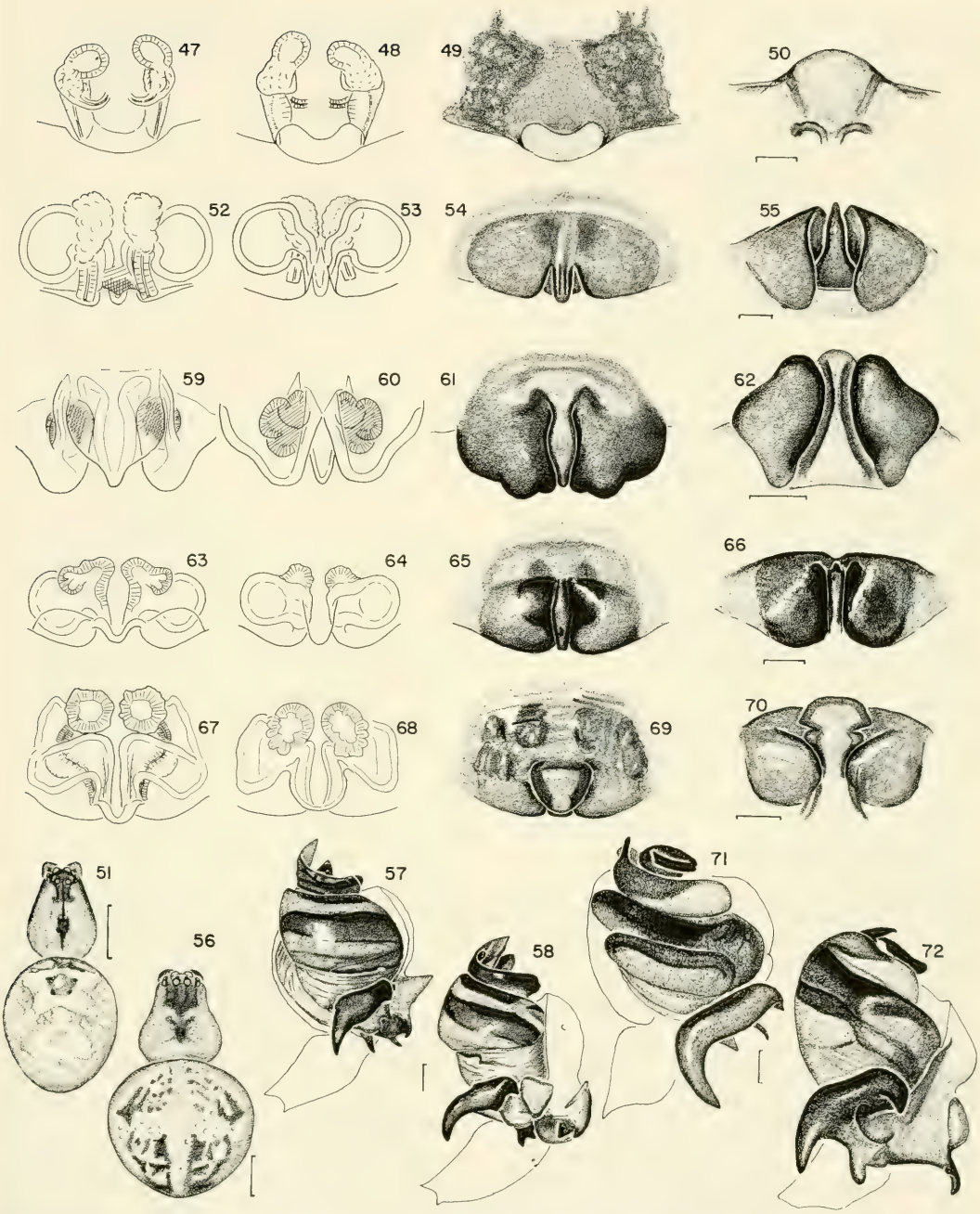
Figures 47–51. *Chrysometa saramacca* n. sp. 47–50. Epigynum. 47. Dorsal, cleared. 48. Ventral, cleared. 49. Ventral. 50. Posterior. 51. Female.

Figures 52–58. *C. hamata* (Bryant). 52–55. Epigynum. 52. Dorsal, cleared. 53. Ventral, cleared. 54. Ventral. 55. Posterior. 56. Female. 57, 58. Left male palpus. 57. Ventral. 58. Lateral.

Figures 59–62. *C. sicki* n. sp., epigynum. 59. Posterodorsal, cleared. 60. Anteroventral, cleared. 61. Ventral. 62. Posterior.



Figures 63–66. *C. malkini* n. sp., epigynum. 63. Dorsal, cleared. 64. Ventral, cleared. 65. Ventral. 66. Posterior.

Figures 67–70. *C. sabana* n. sp., epigynum. 67. Dorsal, cleared. 68. Ventral, cleared. 69. Ventral. 70. Posterior.

Figures 71, 72. *C. raripila* (Keyserling), male palpus. 71. Ventral. 72. Lateral.

Scale lines. 0.1 mm, except Figures 51, 56, 1.0 mm.

Chrysometa raripila (Keyserling), new combination
Figures 71, 72; Map 2

Argyroepeira raripila Keyserling, 1893: 354. pl. 18, fig. 261, ♂. Male from Fazenda Calvarion near Rio de Janeiro, Brazil (BMNH), examined.
Meta raripila:—Roewer, 1942: 920. Bonnet, 1957: 2797 (in part). Not Petrunkevitch, 1930: 339.

Description. Male holotype. Carapace yellow-white with median brown band, narrow at thoracic depression and as wide as posterior median eyes in front. Sternum black. Legs yellow-white. Dorsum of abdomen with posterior transverse dark marks; sides with some silver dots; venter with some black pigment. Eyes subequal in size. Anterior median eyes 0.6 diameters apart, their diameter from laterals. Posterior median eyes 0.8 diameters apart, their diameter from laterals. Total length 3.0 mm. Carapace 1.7 mm long, 1.3 mm wide. First femur, 3.0 mm; patella and tibia, 3.7 mm; metatarsus, 3.2 mm; tarsus, 1.0 mm. Second patella and tibia, 2.6 mm; third, 1.0 mm.

Diagnosis. The T-shape of the paracymbium (Fig. 72) distinguishes this male from others.

Chrysometa linguiformis (Franganillo), new combination
Figures 73–77; Map 2

Meta linguiformis Franganillo, 1930: 20. Six females from Sierra Maestra, Cuba, lost. Franganillo, 1936: 94, fig. 47, ♀. Bonnet, 1957: 2787.
Pseudometa linguiformis:—Bryant, 1940: 353, fig. 128, ♀.
Capichameta linguiformis:—Brignoli, 1983: 227.

Description. Female from Jamaica. Carapace yellow with black marks (Fig. 77); sternum yellow; legs yellow with black spots, fused on underside of first and second femora into longitudinal lines. Dorsum of abdomen gray with black marks and indistinct white spots; venter black with white line on each side. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, slightly more than their diameter from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Abdomen oval. Total length, 4.2 mm. Carapace, 1.8 mm long, 1.5 mm wide. First femur, 2.0 mm; patella and tibia, 2.7 mm; metatarsus, 2.1 mm; tarsus, 0.9 mm. Second patella and tibia, 1.9 mm; third, 1.1 mm; fourth, 1.6 mm.

Variation. Total length of females varies between 4.2 and 5.6 mm.

Diagnosis. This species differs from *C. jayuyensis* by lacking a frame around the median round knob in the epigynum (Fig. 75) and differs from *C. guadeloupensis* by having in posterior view a constriction between the knob and median plate (Fig. 76). In *C. guadeloupensis*, the median plate is separate from the knob.

Distribution. Cuba, Jamaica (Map 2).

Records. CUBA Siboney, shrubs, 26 June 1955, 2♀ (A. F. Archer, AMNH); Gran Piedra, 2 June 1955, 2♀, 29 June 1955, ♀ (A. F. Archer, AMNH); Pan de Palenque, Matanzas, 11 Aug. 1955, 3♀ (A. F. Archer, AMNH); Vega Alta, ♀ (P. Bermudez, CUC); San José, ♀ (MCZ). JAMAICA *St. Ann's Parish:* White River, E of Ocho Rios, coralline limestone, Jan. 1968, ♀ (G. K. Reid, MCZ).

Chrysometa jayuyensis (Petrunkevitch), new combination
Figures 78–84; Map 2

Meta raripila:—Petrunkevitch, 1930: 339, figs. 227–229, ♂. Not *raripila* Keyserling. Misidentification.
Meta jayuyensis Petrunkevitch, 1930: 343. Two female syntypes from coffee plantation at Jayuya, 18°12′N, 66°36′W, 1,150 m el. and one from Bayamón, Puerto Rico (PMY), examined. Roewer, 1942: 919. Bonnet, 1957: 2787.

Description. Female. Carapace yellow-white with gray marks; sternum yellow-white; legs yellow-white with black spots on ventral side. Dorsum of abdomen yellow-white with black marks (Fig. 82) and white pigment spots; venter with gray patch between epigynum and spinnerets, longitudinal gray line on each side with white pigment spots between. Anterior lateral eyes equal to diameter of anterior median eyes; posterior median eyes 1.2

diameters; posterior lateral eyes 0.9 diameters of anterior median eyes. Anterior median eyes 0.8 diameters apart, their diameter from laterals. Posterior median eyes 0.8 diameters apart, slightly more than their diameter from laterals. Total length, 4.3 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 2.2 mm; patella and tibia, 2.7 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.7 mm.

Male. Coloration like female. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, slightly less than their diameter from laterals. Posterior median eyes 0.6 diameters apart, slightly more than their diameter from laterals. Clypeus height 0.7 diameters of anterior median eyes. First femora ventrally with strong macrosetae on tubercles. Abdomen oval. Total length, 3.0 mm. Carapace, 1.6 mm long, 1.2 mm wide. First femur, 2.7 mm; patella and tibia, 3.1 mm; metatarsus, 2.5 mm; tarsus, 0.8 mm. Second patella and tibia, 2.1 mm; third, 0.8 mm; fourth, 1.3 mm.

Variation. Females vary from 3.0 to 4.8 mm total length, males 2.7 mm to 3.2 mm.

Diagnosis. Females can be separated from *C. linguiformis* and *C. guadeloupensis* by having the median knob of the epigynum framed by a fold anteriorly and having a swelling on each side posteriorly (Fig. 80).

Natural History. Specimens were found in a coffee plantation at Jayuya.

Records. PUERTO RICO Guainabo, Oct. 1925, ♀ (A. Petrunkevitch, PMY); Mayagüez, University Farm, 21 Jan. 1962, ♀, 2 Feb. 1964, ♂, Oct. 1964, 3♂ (A. M. Chickering, MCZ); Monte el Estado, Maricao, 9 Jan. 1964, ♂ (A. M. Chickering, MCZ); Bosque Estatal, Maricao, July 1950, 3♀ (A. F. Archer, AMNH); Vivevero de Catalina, Palmer, 17 Feb. 1961, ♀ (A. M. Nadler, AMNH); Maricao, 13 Feb. 1961, ♂ (A. M. Nadler, AMNH); Cafetales, 600–700 m, Castañer, Cord. Central, 22 Aug. 1957, 4♀ (A. F. Archer, AMNH); Salto Collazo, betw. San Sebastian and Lares, 30 July 1950, ♂ (A. F. Archer, AMNH); Aiboneto, 1 June 1915, ♂ (A. Petrunkevitch, AMNH), Jayuya, ca. 1,000 m, 20–26 March 1986, 6♀ (H. L. Levi, MCZ).

Chrysometa guadeloupensis new species
Figures 85–89; Map 2

Holotype. Female holotype, one juvenile paratype in poor condition from Bains Jaunes, in high woods, Guadeloupe, Lesser Antilles, 15 Aug. 1925 (A. Petrunkevitch, PMY). The specific name is an adjective after the type locality.

Description. Female. Carapace yellow-white with brown head (Fig. 89); chelicerae brown; sternum yellow-white; legs with dark rings. Dorsum of abdomen with paired brown marks (Fig. 89), lighter areas with white pigment spots; venter brown with pair of longitudinal light bands. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, slightly less than their diameter from laterals. Posterior median eyes slightly less than their diameter apart, their diameter from laterals. Abdomen spherical. Total length, 5.0 mm. Carapace, 2.4 mm long. First femur, 3.3 mm; patella and tibia, 4.0 mm; metatarsus, 2.9 mm; tarsus, 1.2 mm. Second patella and tibia, 2.9 mm; third, 1.5 mm; fourth, 2.2 mm.

Diagnosis. This species differs from *C. linguiformis* by having the posterior median plate of the epigynum separate from the median knob (Fig. 88).

Chrysometa butamalal new species
Figures 90–94; Map 2

Holotype. Female from Butamalal, 1,100–1,300 m [37°54'S, 73°12'W, Prov. Arauco], Chile, 31 Jan. 1954 (L. Peña, IRSNB). The specific name is a noun in apposition after the locality.

Description. Female. Carapace light orange, head brown, brown area coming to a point on thorax, thoracic rim dusky; sternum dusky brown; legs light orange, indistinctly ringed. Dorsum of abdomen with paired silver spots anteriorly and paired black patches on orange-brown (Fig. 94); sides with scattered silver spots;

venter blackish with two longitudinal lines of silver spots. Eyes subequal in size. Anterior median eyes 0.7 diameters apart, 0.8 diameters from laterals. Posterior median eyes their diameter apart, same distance from laterals. Abdomen oval. Total length, 5.0 mm. Carapace, 1.9 mm long, 1.6 mm wide. First femur, 2.7 mm; patella and tibia, 3.4 mm; metatarsus, 2.4 mm; tarsus, 1.2 mm. Second patella and tibia, 2.5 mm; third, 1.3 mm; fourth, 1.9 mm.

Diagnosis. This species differs from the West Indian *C. linguiformis*, *C. guadeloupensis* and *C. jayuyensis* by having in ventral view the median knob anteriorly attached (Fig. 92) and by having in posterior view no constriction between knob and the median plate (Fig. 93).

Chrysometa plana new species
Figures 95–98; Map 2

Holotype. Female from south of Cuenca, 2,500–2,800 m el., Prov. Azuay, Ecuador, 15 March 1965 (L. Peña, MCZ). The specific name is an arbitrary combination of letters.

Description. Female. Carapace orange-yellow, gray in middle; sternum black; legs orange-yellow. Dorsum of abdomen with white spots and a wide longitudinal black band on posterior half. Venter black with longitudinal line of silver spots on each side. Secondary eyes equal to 1.2 diameters of anterior median eyes. Anterior median eyes their diameter apart, 1.4 diameters from laterals. Posterior median eyes slightly less than their diameter apart, slightly more than their diameter from laterals. Abdomen oval. Total length, 4.2 mm. Carapace, 1.6 mm long, 1.2 mm wide. First femur, 2.3 mm; patella and tibia, 2.9 mm; metatarsus, 2.5 mm; tarsus, 1.0 mm. Second patella and tibia, 1.9 mm; third, 0.9 mm; fourth, 1.5 mm.

Diagnosis. The ventral view of the epigynum, a flat plate with anterior and lateral lips and two posterior lobes (Fig. 97), separates this species from others.

Chrysometa maculata (Bryant), new combination
Figures 99–105; Map 2

Metargyra maculata Bryant, 1945: 388, fig. 15, ♀. Female holotype from Ennery, Haiti (MCZ), examined. Brignoli, 1983: 230

Description. Female. Carapace, sternum orange-yellow. Legs orange-yellow with dark spots on underside. Dorsum of abdomen with dark spots (Fig. 103); sides with indistinct spots; venter with indistinct dark mark on anterior half of area between epigynum and spinnerets. Anterior lateral eyes, posterior median eyes equal to diameter of anterior median eyes; posterior lateral eyes 0.8 diameters of anterior median eyes. Anterior median eyes 0.9 diameters apart, their diameter from laterals. Posterior median eyes 0.8 diameters apart, 1.2 diameters from laterals. Abdomen almost spherical. Total length, 5.0 mm. Carapace, 2.7 mm long, 2.2 mm wide. First femur, 3.2 mm; patella and tibia, 4.1 mm; metatarsus, 2.9 mm; tarsus, 1.2 mm. Second patella and tibia, 3.2 mm; third, 1.6 mm; fourth, 2.5 mm.

Male. Coloration like female, except chelicerae dark brown. Eyes subequal in size. Anterior median eyes 0.9 diameters apart, 0.5 diameters from laterals. Posterior median eyes 0.5 diameters apart, their

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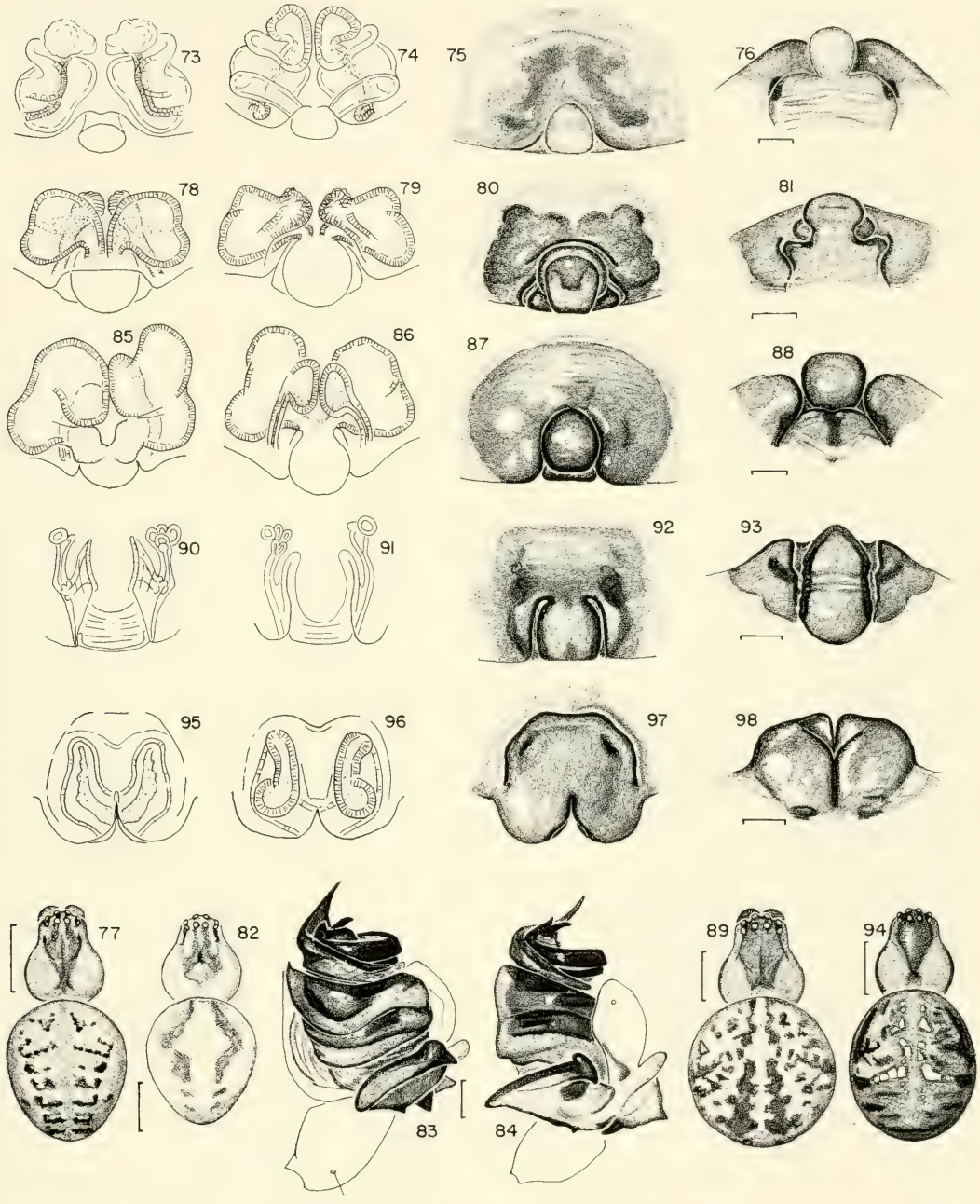
Figures 73–77. *Chrysometa linguiformis* (Franganillo). 73–76. Epigynum. 73. Dorsal, cleared. 74. Ventral, cleared. 75. Ventral. 76. Posterior. 77. Female.

Figures 78-84. *C. jayuyensis* Petrunkevitch. 78–81. Epigynum. 78. Dorsal, cleared. 79. Ventral, cleared. 80. Ventral. 81. Posterior. 82. Female. 83, 84. Left male palpus. 83. Ventral. 84. Lateral.

Figures 85–89. *C. guadeloupensis* n. sp. 85–88. Epigynum. 85. Dorsal, cleared. 86. Ventral, cleared. 87. Ventral. 88. Posterior. 89. Female.



Figures 90–94. *C. butamalal* n. sp. 90–93. Epigynum. 90. Dorsal, cleared. 91. Ventral, cleared. 92. Ventral. 93. Posterior. 94. Female.

Figures 95–98. *C. plana* n. sp., epigynum. 95. Dorsal, cleared. 96. Ventral, cleared. 97. Ventral. 98. Posterior.

Scale lines. 0.1 mm, except Figures 77, 82, 89, 94, 1.0 mm.

diameter from laterals. Legs with strong macrosetae and short, immovable black spines on underside. Total length, 4.4 mm. Carapace, 2.3 mm long, 1.9 mm wide. First femur, 4.2 mm; patella and tibia, 5.4 mm; metatarsus, 4.2 mm; tarsus, 1.3 mm. Second patella and tibia, 4.1 mm; third, 1.5 mm; fourth, 2.3 mm.

Variation. Total length of females varied between 5.0 and 7.4 mm, of males between 4.4 and 5.8 mm.

Diagnosis. Females differ from other species by the vase-shaped septum of the epigynum having openings anterior on the sides (Fig. 101). The male differs from others by the relatively wide tegulum (in ventral view, Fig. 104), the hook-shaped apophysis of the cymbium and the paracymbium with a long, medially pointing "lower" prong (Figs. 104, 105).

Records. DOMINICAN REPUBLIC Cord. Central, Constanza to Garabacoa, 600–1,200 m, Aug. 1938, ♀ (P. J. Darlington, MCZ); Loma Cibao, Cord. Central, La Vega, 1,200–1,700 m, 9 Aug. 1958, ♀, ♂ (A. F. Archer, AMNH). HAITI 40 km from Aux Cayes, 600–1,000 m, 29 Aug. 1935, ♀, ♂ (W. C. Hassler, AMNH).

Chrysometa distincta (Bryant), new combination
Figures 106–112; Map 2

Pseudometa distincta Bryant, 1940: 352, figs. 121, 127. Male holotype and female paratype from south side of Pico Turquino, 3,000–5,000 ft. [1,000–1,600 m], Cuba (MCZ), examined.

Capichameta distincta—Brignoli, 1983: 227.

Note. Bryant (1940) fig. 127 is printed upside down.

Description. Female. Carapace orange-yellow with black V-shaped mark (Fig. 110). Sternum orange-yellow. Legs orange-yellow, ends of articles dark, first and second femora with black patches on anterior. Dorsum of abdomen with paired gray marks and widely scattered silver spots; venter black between epigynum furrow and spinnerets, with black ring around spinnerets. Eyes subequal in size. Anterior median eyes 0.8 diameters apart, their diameter from laterals. Posterior median eyes their diameter apart, their diameter from laterals. Abdomen ovoid. Total length, 3.6 mm. Carapace, 1.7 mm long, 1.3 mm wide. First femur, 1.6 mm; patella and tibia, 2.3 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 1.7 mm; third, 1.1 mm; fourth, 1.4 mm.

Male. Color and structure like female. Total length, 2.6 mm. Carapace, 1.4 mm long, 1.0 mm wide. First femur, 1.8 mm; patella and tibia, 2.2 mm; metatarsus, 1.8 mm; tarsus, 0.8 mm. Second patella and tibia, 1.7 mm; third, 0.9 mm; fourth, 1.2 mm.

Diagnosis. The triangular shape of the septum and transverse bar of the epigynum (Fig. 108) and lobes on each side of the median plate in posterior view (Fig. 109) distinguish females. The male palpus differs by the tightly coiled, relatively short embolus and a long, laterally pointed "lower" prong of the paracymbium (Figs. 111, 112).

Chrysometa nuboso new species
Figures 113–119; Map 2

Holotype. Male holotype and three female paratypes from Bosque Nuboso, Monteverde Cloud Forest Reserve, 580 m el., Prov. Puntarenas, Costa Rica, 22 July 1979 (C. L. Craig, P. K. Klass, MCZ). The specific name is a noun apposition after the type locality.

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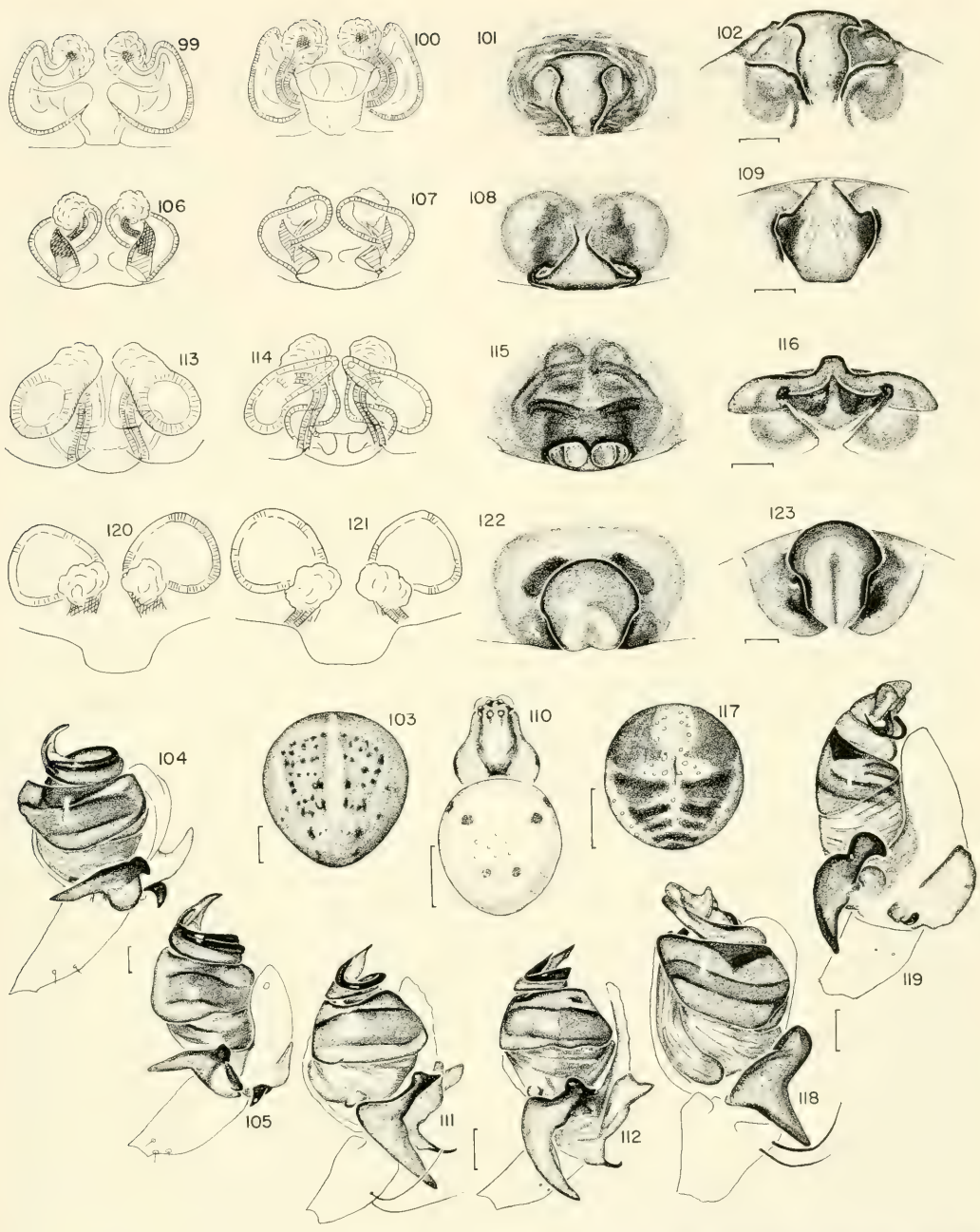
Figures 99–105. *Chrysometa maculata* (Bryant). 99–102. Epigynum. 99. Dorsal, cleared. 100. Ventral, cleared. 101. Ventral. 102. Posterior. 103. Female abdomen, dorsal. 104, 105. Left male palpus. 104. Ventral. 105. Lateral.

Figures 106–112. *C. distincta* (Bryant). 106–109. Epigynum. 106. Dorsal, cleared. 107. Ventral, cleared. 108. Ventral. 109. Posterior. 110. Female. 111, 112. Male palpus. 111. Ventral. 112. Lateral.



Figures 113–119. *C. nuboso* n. sp.113–116. Epigynum. 113. Dorsal, cleared. 114. Ventral, cleared. 115. Ventral. 116. Posterior. 117. Female abdomen, dorsal. 118, 119. Male palpus. 118. Ventral. 119. Lateral.

Figures 120–123. *C. keyserlingi* n. sp., epigynum. 120. Dorsal, cleared. 121. Ventral, cleared. 122. Ventral. 123. Posterior.

Scale lines. 0.1 mm, except Figures 103, 110, 117, 1.0 mm.

Description. Female. Carapace, sternum, legs yellow; distal ends of leg articles darker. Dorsum of abdomen with white pigment spots and indistinct transverse dark marks on posterior (Fig. 117). Anterior lateral eyes, posterior median eyes equal to diameter of anterior medians; posterior lateral eyes 0.8 diameters of anterior medians. Anterior median eyes 0.8 diameters apart, 0.6 diameters from laterals. Posterior median eyes 0.6 diameters apart, their diameter from laterals. Abdomen spherical. Total length, 3.6 mm. Carapace, 2.0 mm long, 1.4 mm wide. First femur, 2.3 mm; patella and tibia, 2.9 mm; metatarsus, 2.2 mm; tarsus, 1.1 mm. Second patella and tibia, 2.0 mm; third, 1.1 mm; fourth, 1.4 mm.

Male. Carapace yellow, posteriorly dusky in middle; head orange. Sternum, legs yellow. Dorsum of abdomen with some gray on sides. Anterior lateral eyes and posterior median eyes equal to diameter of anterior medians; posterior laterals 0.8 diameters of anterior median eyes. Anterior median eyes 0.8 diameters apart, 0.6 from laterals. Posterior median eyes 0.7 diameters apart, their diameter from laterals. Total length, 4.0 mm. Carapace, 2.2 mm long, 1.7 mm wide. First femur, 3.6 mm; patella and tibia, 4.3 mm; metatarsus, 3.8 mm; tarsus, 1.3 mm. Second patella and tibia, 3.0 mm; third, 1.3 mm; fourth, 1.9 mm.

Variation. Total length of females varies from 3.6 to 4.0 mm, males from 3.4 to 3.8 mm.

Diagnosis. The epigynum distinguishes this species by the septum whose anterior lateral margins continue laterally to frame the depression and by the posterior transverse bar which turns anterior and widens on each side (Fig. 115). In ventral view the "lower" prong of the paracymbium is pointed and at an angle (Fig. 118), in lateral view the "upper" prong is curved (Fig. 119).

Paratypes. COSTA RICA *Prov. Puntarenas:* Monteverde, cloud forest, 1,580–1,600 m, 1977–1978, 9 collections, 8♀, 2♂ (C. L. Craig, P. Klass, MCZ, AMNH, BMNH, USNM, SMF); Monteverde, Guindon property, around house, 580 m, July 1978, 2♀, ♂ (C. L. Craig, P. Klass, MCZ).

Chrysometa keyserlingi new species
Figures 120–126; Map 2

Holotype. Male from San Javier, San Pedro, 1,560 m, Sierra Nevada de Santa Marta, Dpto. Magdalena, Colombia, 29 March 1975 (J. A. Kochalka, MCZ). This species is named after Count E. Keyserling, who named many species of *Chrysometa.*

Description. Female. Carapace, sternum, legs yellow. Abdomen with large silver spots and a scattering of tiny black pigment spots (Fig. 124). Posterior median and anterior lateral eyes 1.2 diameters of anterior medians, posterior laterals subequal. Anterior median eyes their diameter apart, 1.2 from laterals. Posterior median eyes slightly less than their diameter apart, 1.3 from laterals. The abdomen is narrow oval (Fig. 124). Total length 4.5 mm, carapace 2.1 mm long, 1.7 mm wide. Second patella and tibia, 2.9 mm; third, 1.5 mm; fourth, 2.2 mm.

Male. Carapace, sternum, legs yellow-white, black on each side of thorax; first coxa and femur black except for distal end. Dorsum of abdomen with black marks and scattered silver spots; venter yellow with some silver spots. Lateral eyes equal to 0.8 diameters of anterior medians; posterior median eyes equal to diameter of anterior median eyes. Anterior median eyes their diameter apart, 0.7 diameters from laterals. Posterior median eyes their diameter apart, slightly less than their diameter from laterals. Abdomen elongate, slightly constricted in middle. Total length, 3.7 mm. Carapace, 1.7 mm long, 1.3 mm wide. First femur, 5.8 mm; patella and tibia, 7.2 mm; metatarsus, 7.9 mm; tarsus, 1.8 mm. Second patella and tibia, 3.9 mm; third, 1.7 mm; fourth, 2.7 mm.

Diagnosis. The female differs from other species with a round median knob-like septum in the epigynum (Fig. 122) by having a lateral constriction and a median groove on the posterior face of the median

plate (Fig. 123). The male is distinguished from others by the long palpal tibia and a wide, distally notched conductor (Figs. 125, 126).

Note. Male and female were collected together 40 km SW Mokoa, Colombia.

Natural History, Distribution. Found at intermediate altitudes, northern and central Colombia (Map 2).

Paratypes. COLOMBIA Bogotá, ♀ (with syntypes of *C. rubromaculata,* BMNH). *Dpto. Nariño:* 40 km SW Mokoa, 3 March 1955, ♀, ♂ (E. S. Ross, E. I. Schlinger, CAS).

Chrysometa donachui new species
Figures 127–133; Map 2

Holotype. Female with male and one female paratypes from Río Donachui, 4,000 m, timberline, Sierra Nevada de Santa Marta, Colombia, 18 Jan. 1974 (J. A. Kochalka, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow with black V-shaped mark; sternum black; legs ringed. Dorsum of abdomen with black marks (Fig. 131), no silver spots; venter black with colorless longitudinal line on each side. Secondary eyes equal to 1.2 diameters of anterior median eyes. Anterior median eyes 1.3 diameters apart, same distance from laterals. Posterior median eyes their diameter apart, 1.2 diameters from laterals. Abdomen subspherical. Total length, 4.6 mm. Carapace, 1.8 mm long, 1.5 mm wide. First femur, 2.8 mm; patella and tibia, 3.4 mm; metatarsus, 2.5 mm; tarsus, 1.1 mm. Second patella and tibia, 2.3 mm; third, 1.1 mm; fourth, 1.7 mm.

Male. Coloring, eye position like female. Total length, 4.0 mm. Carapace, 2.0 mm long, 1.6 mm wide. First femur, 3.7 mm; patella and tibia, 4.7 mm; metatarsus, 4.5 mm; tarsus, 1.3 mm. Second patella and tibia, 2.7 mm; third, 1.3 mm; fourth, 2.1 mm.

Diagnosis. The epigynum of *C. donachui* differs from that of *C. marta* and *C. sondo* in having anteriorly on each side of the median knob an opening surrounded by a lip (Fig. 129). The male can be separated from others by the relatively short embolus of the palpus and by the paracymbium having three curved teeth (Figs. 132, 133).

Records. COLOMBIA *Dpto. Magdalena,* Sierra Nevada de Santa Marta: Casa Antonio, Loma Cebolleta, 2,700 m, low vegetation, 8 May 1975, 8♀, ♂ (MCZ), 15 Feb. 1974, ♀ (AMNH); Loma Cebolleta, 3,500 m, 9 May 1975, ♂ (BMNH); Río Donachui, 2,800 m, 2 Jan. 1975, ♀ (BMNH) Río Donachui, 3,000 m, 19 Jan. 1974, ♀ (IBNA); Cerro Cinaí, 2,500 m, 27 April 1975, ♀ (USNM); 2,600 m, 26 April 1975, ♀ (IBNA); nr. Lower Twin Lake, Que. el Chorro, 3,600 m, 3 March 1975, ♂ (AMNH); old hut, Serra Nueva Granada, 2,500 m, 26 April 1975, 2♀, 2♂ (MCZ, all J. A. Kochalka).

Chrysometa marta new species
Figures 134–137; Map 2

Holotype. Female from Casa Antonia, Loma Cebolleta, 2,700 m, Sierra Nevada de Santa Marta, Dpto. Magdalena, Colombia, 15 Feb. 1974 (J. Kochalka, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange with dark V-shaped mark on thoracic depression; sternum orange; legs orange-white. Dorsum of abdomen orange-white with black patch on shoulders continuing posteromedially into black line, posteriorly with median black band with parallel margins; venter without markings. Eyes subequal in size. Anterior median eyes 1.2 diameters apart, 2 diameters from laterals. Posterior median eyes 1.2 diameters apart, 1.5 diameters from laterals. Abdomen subspherical. Total length, 4.0 mm. Carapace, 1.6 mm long, 1.2 mm wide. First femur, 2.0 mm; patella and tibia, 2.3 mm; metatarsus, 2.1 mm; tarsus, 0.8 mm. Second patella and tibia, 1.5 mm; third, 0.8 mm; fourth, 1.2 mm.

Diagnosis. Chrysometa marta differs from *C. sondo* and *C. donachui* by having the opening located anteriolaterally of the median knob behind a transverse posterior lip (Fig. 136).

Paratype. COLOMBIA *Dpto. Magdalena:* Sierra Nevada de Santa Marta, Río Donachui trail, 2,400–2,800 m, 2 Jan. 1973, ♀ (J. Kochalka, MCZ).

Chrysometa sondo new species
Figures 138–142; Map 2

Holotype. Female holotype with five female paratypes from path from Pilimbalá to Volcán Puracé, 3,690 m, Parque Nacional Puracé, Dpto. Cauca, Colombia, 12–13 Jan. 1983 (J. Kochalka, MCZ). The specific name is an arbitrary combination of letters.

Description. Female. Carapace orange with black marks; sternum black; legs orange with black rings. Dorsum of abdomen with silver spots and black marks (Fig. 142); sides with silver spots and black streaks; venter black, light line containing silver spots on each side. Secondary eyes equal to 1.3 diameters of anterior median eyes. Anterior median eyes their diameter apart, same distance from laterals. Posterior median eyes slightly less than their diameter apart, slightly more than their diameter from laterals. Abdomen subspherical with small shoulder humps (Fig. 142). Total length, 4.5 mm. Carapace, 1.5 mm long, 1.3 mm wide. First femur, 2.2 mm; patella and tibia, 2.7 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 1.6 mm; third, 0.9 mm; fourth, 1.4 mm.

Diagnosis. This species is distinguished from *C. marta* and *C. sevillano* by an indistinct depression on the anterior end of each side of the median septum of the epigynum (Fig. 140).

Chrysometa nigroventris (Keyserling), new combination
Figures 143–146

Meta nigroventris Keyserling, 1880: 316, pl. 4, fig. 17, ♂. Three male syntypes from New Granada [Spanish colony of Colombia and Panama] (BMNH), examined, and labeled syntypes.

Argyroepeira nigroventris:—Keyserling, 1893: 350, pl. 18, fig. 258.

Leucauge nigroventris:—Roewer, 1942: 1011. Bonnet, 1957: 2472.

Note. Keyserling described a female but pictured a male palp. Female is a misprint since the original specimens of Keyserling were males. A small pencil label in the type vial reads "not types," apparently written by Pocock who saw Keyserling's description of a female and who also inserted a BMNH India ink label: *Meta nigroventris* when curating the collections.

Description. Male syntype. Carapace, legs light orange. Labium, sternum black (Fig. 144). Dorsum of abdomen with a band of silver spots on each side, black transverse patches posteriorly, and some silver spots anteriorly, but with distinct median longitudinal gray line; venter black with two wide silver parallel lines (Figs. 143, 144). Eyes subequal in size. Anterior median eyes 0.8 diameters apart, 0.8 from laterals. Posterior median eyes 0.9 diameters apart, 1.1 from laterals. Abdomen oval. Total length 2.5 mm. Carapace 1.3 mm long, 0.9 mm wide. First femur 1.9 mm long; patella and tibia, 2.3 mm; metatarsus, 1.8 mm; tarsus, 0.5 mm. Second patella and tibia, 1.4 mm; third, 0.5 mm; fourth, 1.0 mm.

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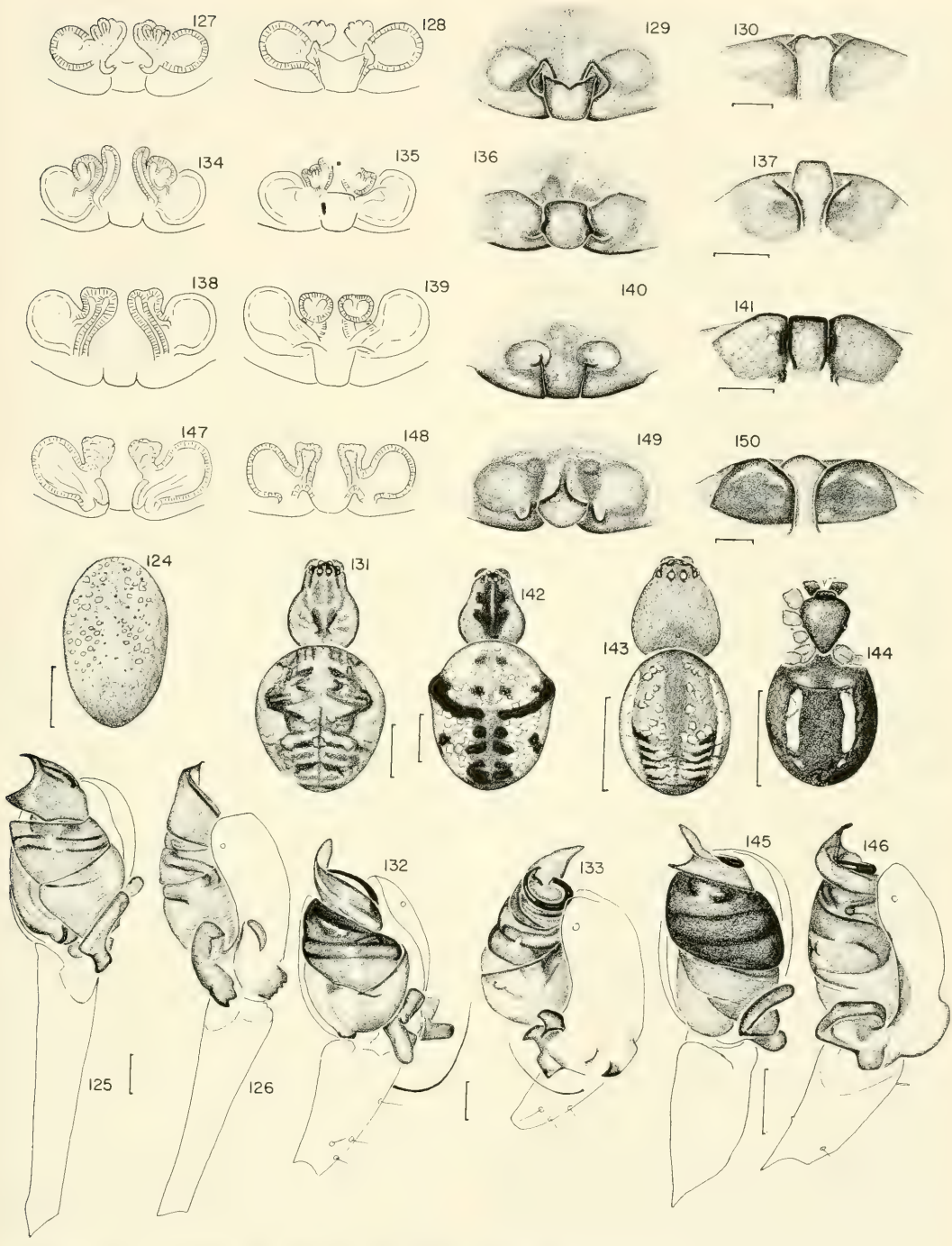
Figures 124–126. *Chrysometa keyserlingi* n. sp. 124. Female abdomen, dorsal. 125, 126. Left male palpus. 125. Ventral. 126. Lateral.

Figures 127–133. *C. donachui* n. sp. 127–130. Epigynum. 127. Dorsal, cleared. 128. Ventral, cleared. 129. Ventral. 130. Posterior. 131. Female. 132, 133. Male palpus. 132. Ventral. 133. Lateral.

Figures 134–137. *C. marta* n. sp., epigynum. 134. Dorsal, cleared. 135. Ventral, cleared. 136. Ventral. 137. Posterior.

Figures 138–142. *C. sondo* n. sp. 138–141. Epigynum. 138. Dorsal, cleared. 139. Ventral, cleared. 140. Ventral. 141. Posterior. 142. Female.

Figures 143–146. *C. nigroventris* (Keyserling). 143, 144. Male. 143. Dorsal. 144. Ventral. 145, 146. Male palpus. 145. Ventral. 146. Lateral.



Figures 147–150. *C. sevillano* n. sp., epigynum. 147. Dorsal, cleared. 148. Ventral, cleared. 149. Ventral. 150. Posterior. *Scale lines.* 0.1 mm, except Figures 124, 131, 142–144, 1.0 mm.

Diagnosis. The palpus has a much shorter tibia (Figs. 145, 146) than *C. keyserlingi* and in lateral view a fan-shaped paracymbium with a small knob below (Fig. 146).

Chrysometa sevillano new species
Figures 147–150; Map 2

Holotype. Female holotype and one female paratype from N. Río Sevillano, 3,700 m, Sierra Nevada de Santa Marta, Colombia, 11 Feb. 1974 (J. A. Kochalka, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow with black V-shaped mark; sternum black; legs yellow with indistinct black rings. Dorsum of abdomen without silver spots, markings like *C. donachui.* Secondary eyes equal to 1.2 diameters of anterior medians. Anterior median eyes slightly more than their diameter apart, same distance from laterals. Posterior median eyes 0.8 diameters apart, 1.3 diameters from laterals. Abdomen oval. Total length, 5.0 mm. Carapace, 2.1 mm long, 1.9 mm wide. First femur, 3.4 mm; patella and tibia, 4.2 mm; metatarsus, 3.3 mm; tarsus, 1.3 mm. Second patella and tibia, 2.7 mm; third, 1.3 mm; fourth, 2.3 mm.

Diagnosis. This species is slightly larger than the similar *C. donachui*; the abdomen is more oval, and the median knob of the epigynum has an anterior stalk (Fig. 149).

Records. COLOMBIA *Dpto. Magdalena*, Sierra Nevada de Santa Marta: Loma Cebolleta, 3,500 m, 9 May 1975, 6♀ (J.A. Kochalka, AMNH, BMNH, IBNA, MCZ, USNM).

Chrysometa chulumani new species
Figures 151–154; Map 2

Holotype. Female from Chulumani, 1,700 m, Yungas, Dpto. La Paz, Bolivia, 17–25 Dec. 1955 (L. Peña, IRSNB). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, legs light orange. Abdomen evenly covered with small silver spots about their diameter apart. Eyes subequal in size. Anterior median eyes their diameter apart, slightly more than their diameter from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Abdomen subspherical. Total length, 4.4 mm. Carapace, 1.8 mm long, 1.4 mm wide. First femur, 2.8 mm; patella and tibia, 3.4 mm; metatarsus, 2.9 mm; tarsus, 0.9 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.7 mm.

Diagnosis. This species differs from *C. serachui* and *C. adelis* and others by the epigynum having a septum and a square posterior transverse bar with the depressions on each side of the septum and with the septum and bar occupying an area longer than wide (Fig. 153).

Chrysometa adelis new species
Figures 155–159; Map 2

Holotyope. Female from above Fidelia, ca. 2,000 m, Dept. Valle, Colombia, 28 February 1969 (W. Eberhard, MCZ). The name is an arbitrary combination of letters.

Description. Female. Carapace orange, head and thorax darker; sternum orange with some gray; legs orange, indistinctly ringed. Dorsum of abdomen with black marks and tiny silver spots on sides; sides silver, black towards venter; venter black with two thin silver longitudinal lines (Fig. 159). Eyes subequal in size. Anterior median eyes 0.8 diameters apart, 1.2 diameters from laterals. Posterior median eyes 0.8 diameters apart, their diameter from laterals. Abdomen narrow oval (Fig. 159). Total length, 5.8 mm. Carapace, 2.5 mm long, 1.9 mm wide. First femur, 5.2 mm; patella and tibia, 6.3 mm; metatarsus, 6.2 mm; tarsus, 1.7 mm. Second patella and tibia, 3.8 mm; third, 1.9 mm; fourth, 2.9 mm.

Diagnosis. The species differs from *C. schneblei* by having the diagonal slits on each side of the median septum of the epigynum shorter and the depressions not bordered (Fig. 157).

Paratypes. Two ♀ from type locality, 2 Dec. 1969 (W. Eberhard, MCZ).

Chrysometa schneblei new species
Figures 160–164; Map 2

Holotype. Female from Medellín, 1,700 m, Dept. Antioquia, Colombia, Jan. 1964 (P. B. Schneble, MCZ). The species is named after the collector, Father Schneble.

Description. Female. Carapace orange-yellow with gray markings (Fig. 164); sternum with gray pigment on orange; legs orange-yellow with indistinct gray rings. Dorsum of abdomen with gray marks on white pigment spots (Fig. 164); venter black between epigynum and spinnerets, with a white line on each side. Secondary eyes equal to 1.3 diameters of anterior median eyes. Anterior median eyes 1.2 diameters apart, 1.2 diameters from laterals. Posterior median eyes 0.8 diameters apart, slightly more than their diameter from laterals. Abdomen oval (Fig. 164). Total length, 4.2 mm. Carapace, 1.6 mm long, 1.2 mm wide. First femur, 2.7 mm; patella and tibia, 3.3 mm; metatarsus, 2.6 mm; tarsus, 0.9 mm. Second patella and tibia, 2.0 mm; third, 1.0 mm; fourth, 1.6 mm.

Note. The epigynum is filled with a plug which cannot be removed.

Diagnosis. This species differs from *C. adelis* by longer, diagonal slits on each side of the median septum of the epigynum and by having the depressions anteriorly surrounded by a lip (Fig. 162).

Natural History, Distribution. Found 1,800 to 3,000 m, central Colombia, Ecuador (Map 2).

Paratypes. COLOMBIA *Dpto. Cundinamarca:* Monterodondo, 3,000 m, 30 Jan. 1975, 5♀ (A. Schneble, MCZ). *Valle:* above Habana, 2,200 m, 16 Sept. 1969, ♀ (W. Eberhard, MCZ). ECUADOR *Prov. Imbabura:* Otavalo-Apuela, 2,200 m, 8–9 Sept. 1977, ♀ (L. Peña, AMNH). *Loja:* Zamora, 1,800–2,200 m, 28 Oct. 1977, ♀ (L. Peña, AMNH).

Chrysometa serachui new species
Figures 165–169; Map 2

Holotype. Female from Serachui, 1,600 m, Sierra Nevada de Santa Marta, Colombia, 27 Dec. 1973 (J. A. Kochalka, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow with indistinct gray V-shaped mark; sternum gray on orange; legs yellow, indistinctly ringed. Dorsum of abdomen with indistinct gray marks and white spots; venter gray with colorless band on each side, bands widest posteriorly (Fig. 169). Eyes subequal in size. Anterior median eyes their diameter apart, 1.3 diameters from laterals. Posterior median eyes slightly less than their diameter apart, slightly more than their diameter from laterals. Abdomen oval. Total length, 4.2 mm. Carapace, 1.6 mm long, 1.4 mm wide. First femur, 2.9 mm; patella and tibia, 3.4 mm; metatarsus, 2.9 mm; tarsus, 0.9 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.6 mm.

Diagnosis. This species differs from *C. sevillano* and *C. sondo* by having the openings of the epigynum midway along the side of the median septum (Fig. 167).

Paratypes. COLOMBIA *Dpto. Magdalena*, Sierra Nevada de Santa Marta: Serra Nueva Granada, 2,000 m, 7 April 1975, ♀, 2 imm. (J. A. Kochalka, MCZ). W of Cerro Bucuncusa, 1,800 m, 29 Dec. 1973, ♀ (J. A. Kochalka, AMNH).

Chrysometa banos new species
Figures 170–174; Map 2

Holotype. Female from Baños, 2,200 m el., Prov. Tungurahua, Ecuador, April 1939 (W. C. Macintyre, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange-yellow; sternum, legs dark brown. Dorsum of abdomen with scattered white spots more than their diameter apart (Fig. 174); venter with longitudinal black band between epigynum and spinnerets. Eyes subequal in size. Anterior median eyes their diameter apart, 1.2 diameters from laterals. Posterior median eyes 0.8 diameters apart, their diameter from laterals. Abdomen oval (Fig. 174). Total length, 5.2 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 2.9 mm; patella and

tibia, 3.8 mm; metatarsus, 3.1 mm; tarsus, 1.1 mm. Second patella and tibia, 2.4 mm; third, 1.2 mm; fourth, 1.8 mm.

Diagnosis. This species differs from *C. satulla* by having the openings of the epigynum at the ends of diagonal grooves (Fig. 172); *C. banos* is smaller than *C. adelis* and has a wider abdomen than *C. schneblei.*

Chrysometa satulla (Keyserling), new combination
Figures 175–179; Map 2

Meta satulla Keyserling, 1880: 556, pl. 16, fig. 7, ♀. Female holotype in shriveled condition from Paltaypampa [1,800 m, Dpto. Junín, Prov. Tarma], Peru (PAN), examined. Roewer, 1942, Katalog der Araneae, 1: 920. Bonnet, 1957: 2797.

Argyroepeira satulla:—Keyserling, 1893: 339, pl. 17, fig. 250, ♀.

Note. Female holotype is dark and shriveled. It may once have been dried.

Description. Female. Carapace dark orange. Sternum darker than coxae. Legs orange. Dorsum of abdomen silver with black on each anterior dorsal side, silver in between, median posterior longitudinal dark band containing paired black patches (Fig. 179); venter with silver patch on each side, closer to spinnerets than epigynum, and a median dark longitudional band and silver specks here and there on sides. Eyes subequal in size. Anterior median eyes their diameter apart, 1.2 mm from laterals. Posterior median eyes slightly less than their diameter apart, their diameter from laterals. Abdomen probably oval [shriveled now], shield-shaped, almost as wide as long, with anterior humps. Total length, 3.3 mm. Carapace, 1.3 mm long, 1.0 mm wide. First femur, 2.2 mm; patella and tibia, 2.6 mm; metatarsus, 2.3 mm; tarsus, 0.8 mm. Second patella and tibia, 1.5 mm; third, 0.9 mm; fourth, 1.2 mm.

Diagnosis. This species is distinguished from *C. banos* by having a wider septum and transverse bar in the epigynum and by having the openings in circular depressions (Fig. 177).

Chrysometa lepida (Keyserling), new combination
Figures 180–184; Map 2

Meta lepida Keyserling, 1882: 273, pl. 11, fig. 3, ♀, ♂. Male and two female syntypes from Pumamarca, 1,900 m el., Prov. Tarma, Dpto. Junín, Peru (PAN), examined. Roewer, 1942: 919.

Argyroepeira lepida:—Keyserling, 1893: 327, pl. 17, fig. 242, ♀, ♂.

Leucauge lepida:—Bonnet, 1957: 2470.

Note. The type specimens are in poor physical condition. The internal female genitalia were illustrated in dorsal view only by clearing with clove oil.

Description. Female. Carapace, sternum, legs orange-yellow. Dorsum of abdomen with silver spots; black spot on each side anterior lateral; venter and posterior above spinnerets without spots. Anterior median eyes slightly smaller than others. Anterior median eyes their diameter apart, 2.5 from laterals. Posterior median eyes their diameter apart, 1.5 from laterals. Total length, 2.9 mm. Carapace, 1.3 mm

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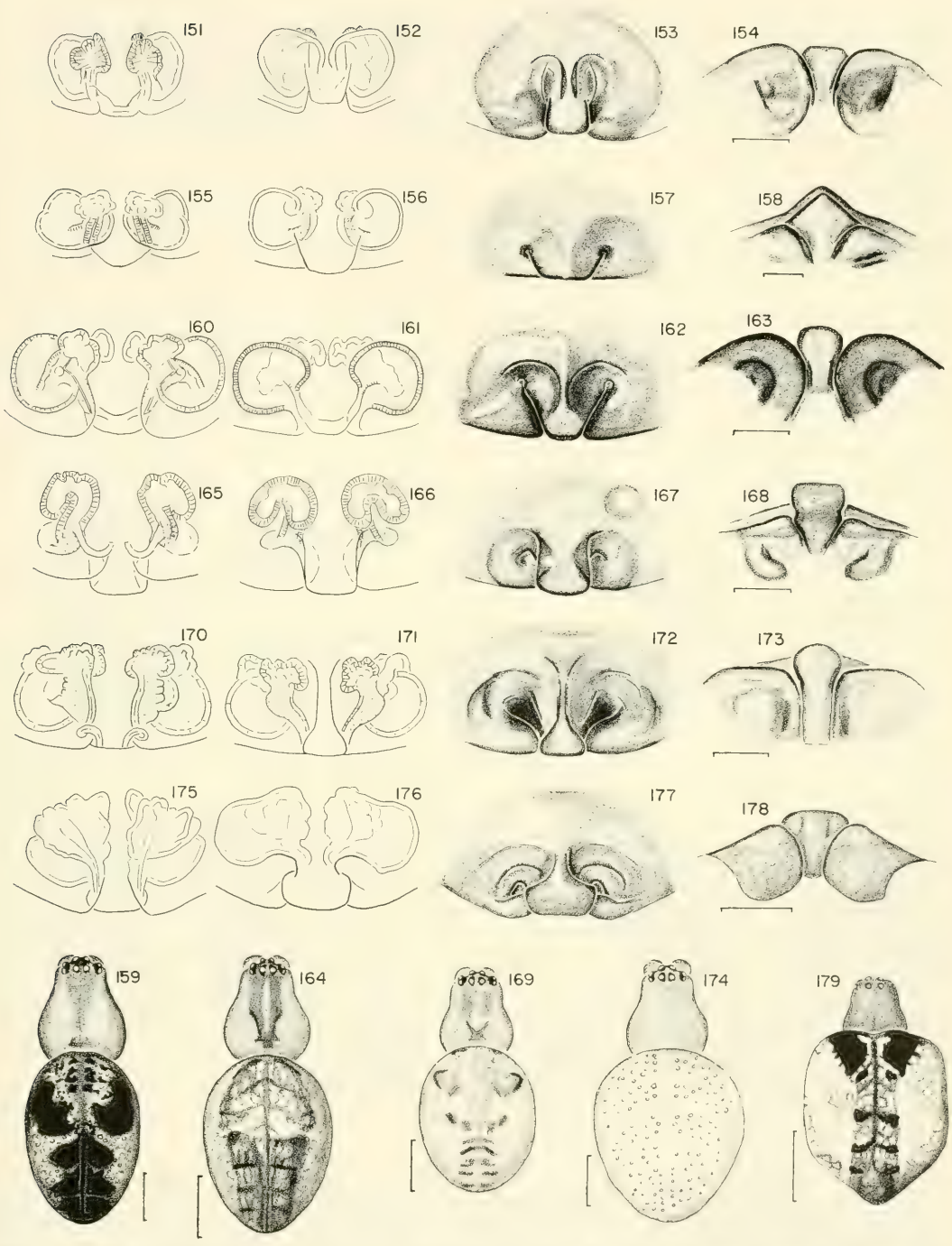
Figures 151–154. *Chrysometa chulumani* n. sp., epigynum. 151. Dorsal, cleared. 152. Ventral, cleared. 153. Ventral. 154. Posterior.

Figures 155–159. *C. adelis* n. sp. 155–158. Epigynum. 155. Dorsal, cleared. 156. Ventral, cleared. 157. Ventral. 158. Posterior. 159. Female.

Figures 160–164. *C. schneblei* n. sp. 160–163. Epigynum. 160. Dorsal, cleared. 161. Ventral, cleared. 162. Ventral. 163. Posterior. 164. Female.

Figures 165–169. *C. serachui* n. sp. 165–168. Epigynum. 165. Dorsal, cleared. 166. Ventral, cleared. 167. Ventral. 168. Posterior. 169. Female.

Figures 170–174. *C. banos* n. sp. 170–173. Epigynum. 170. Dorsal, cleared. 171. Ventral, cleared. 172. Ventral. 173. Posterior. 174. Female.



Figures 175–179. *C. satulla* (Keyserling). 175–178. Epigynum. 175. Dorsal, cleared. 176. Ventral, cleared. 177. Ventral. 178. Posterior. 179. Female.

Scale lines. 0.1 mm, except Figures 159, 164, 169, 174, 179, 1.0 mm.

long, 1.2 mm wide. First femur, 1.7 mm; patella and tibia, 1.9 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm. Second patella and tibia, 1.5 mm; third, 0.8 mm; fourth, 1.0 mm.

Male. Coloration like female. Total length, 2.0 mm. Carapace, 1.2 mm long, 0.9 mm wide. First femur, 1.8 mm; patella and tibia, 2.0 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm. Second patella and tibia, 1.6 mm; third, 0.7 mm; fourth, 1.0 mm.

Diagnosis. The epigynum differs from that of related species by lacking a depression in ventral view and having three posterior lobes (Figs. 181, 182). The male differs from others by the tight coil of the short palpal embolus, the shape of the paracymbium (Figs. 183, 184) and by the two teeth on the base of the cymbium (Fig. 184).

Chrysometa boquete new species
Figures 185–191; Map 2

Holotype. Female holotype and three female, one male paratypes from Boquete, Chiriquí Prov., Panama, Aug. 1950 (A. M. Chickering, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange; chelicerae brown; sternum black on orange. Legs orange with black rings on distal ends of tibiae. Dorsum of abdomen with silver spots, black shoulder patches, and posterior black transverse marks (Fig. 189); sides black; venter with triangular black mark pointing to spinnerets, and a patch with silver spots on each side posteriorly; black around spinnerets. Anterior lateral eyes and posterior median eyes equal to 1.2 diameters of anterior medians; posterior laterals equal to diameter of anterior medians. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes their diameter apart, 1.2 diameters from laterals. Total length, 3.5 mm. Carapace, 1.4 mm long, 1.2 mm wide. First femur, 2.1 mm; patella and tibia, 2.4 mm; metatarsus, 2.1 mm; tarsus, 0.7 mm. Second patella and tibia, 1.6 mm; third, 0.9 mm; fourth, 1.3 mm.

Male. Coloration like female but darker. Venter of abdomen with pair of silver patches anterior of spinnerets. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, slightly less than their diameter from laterals. Posterior median eyes their diameter apart, 1.2 diameters from laterals. Abdomen elongate oval. Total length, 2.4 mm. Carapace, 1.2 mm long, 1.0 mm wide. First femur, 2.5 mm; patella and tibia, 3.0 mm; metatarsus, 2.7 mm. Second patella and tibia, 1.7 mm; third, 0.8 mm; fourth, 1.3 mm.

Variation. Total length of females varied from 2.8 to 3.5 mm, of males from 2.4 to 2.9 mm.

Diagnosis. The female differs from related species by having the median septum of the epigynum wider than long with the openings posterior on each side (Fig. 187). The male differs from *C. aramba* by having a tightly wound short embolus (Figs. 190, 191) and by having the "lower" end of the paracymbium rounded and corniculate (Fig. 190).

Natural History, Distribution. Found from 1,500 to 3,300 m, western Panama, Colombia (Map 2).

Paratypes. PANAMA *Prov. Chiriquí:* Boquete, Aug. 1950, 3♀, ♂ (A. M. Chickering, MCZ); Volcán, 26 Feb. 1936, 4♀, 2♂ (W. J. Gertsch, AMNH). COLOMBIA Bo-

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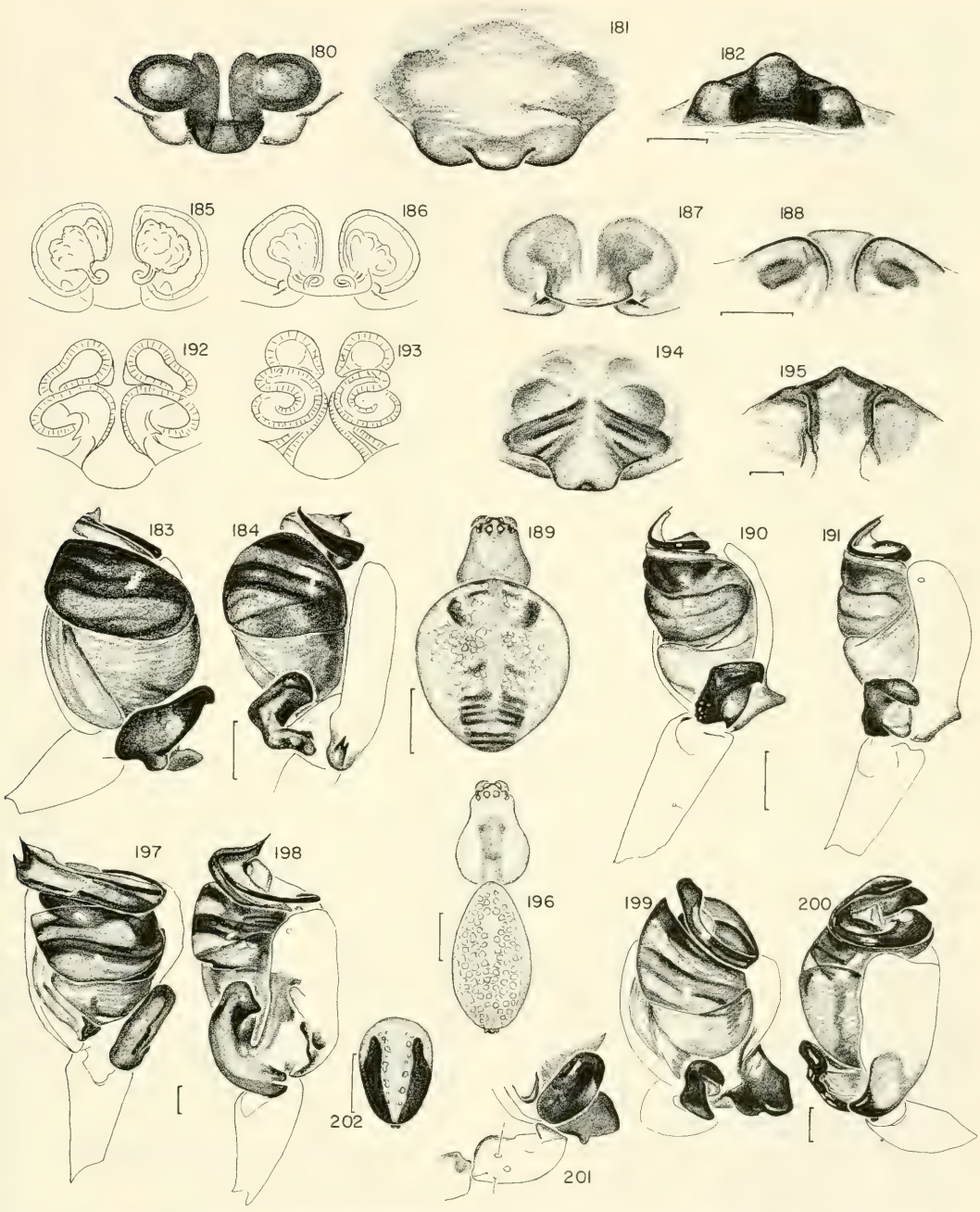
Figures 180–184. *Chrysometa lepida* (Keyserling). 180–182. Epigynum. 180. Dorsal. 181. Ventral. 182. Posterior. 183, 184. Left male palpus. 183. Ventral. 184. Lateral.

Figures 185–191. *C. boquete* n. sp. 185–188. Epigynum. 185. Dorsal, cleared. 186. Ventral, cleared. 187. Ventral. 188. Posterior. 189. Female. 190, 191. Male palpus. 190. Ventral. 191. Lateral.



Figures 192–198. *C. saladito* n. sp. 192–195. Epigynum. 192. Dorsal, cleared. 193. Ventral, cleared. 194. Ventral. 195. Posterior. 196. Female. 197, 198. Male palpus. 197. Ventral. 198. Lateral.

Figures 199–202. *C. lapazensis* n. sp. 199–201. Male palpus. 199. Ventral. 200. Lateral. 201. Paracymbium and patella, ventral. 202. Male abdomen, dorsal.

Scale lines. 0.1 mm, except Figures 189, 196, 202, 1.0 mm.

gotá, Coachi Rd., 3,300 m, 19 July 1967, ♀ (P., B. Wygodzinsky, AMNH).

Chrysometa saladito new species
Figures 192–198; Map 2

Holotype. Male holotype and female paratype from near Saladito, 1,000 m el., Dpto. Valle, Colombia (W. Eberhard, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow-white with orange patch on middle; no black pigment around eyes. Sternum yellow-white. Legs yellow-white, distal gray rings around ends of tibiae, metatarsi, and tarsi. Dorsum and sides of abdomen with large silver spots (Fig. 196); venter with silver spots, except for epigastric area and around spinnerets. Posterior median eyes equal to diameter of anterior medians; lateral eyes 0.8 diameters of anterior median eyes. Anterior median eyes their diameter apart, their diameter from laterals; posterior median eyes slightly more than their diameter apart, the same distance from laterals. Total length, 4.5 mm. Carapace, 2.0 mm long, 1.5 mm wide. First femur, 4.3 mm; patella and tibia, 4.6 mm; metatarsus, 4.6 mm; tarsus, 1.4 mm. Second patella and tibia, 3.2 mm; third, 1.7 mm; fourth, 2.4 mm.

Male. Carapace yellow with black pigment around edge and a wide brown band on sides of thorax; no orange patch. Eyes subequal in size. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes slightly more than their diameter apart, the same distance from laterals. Total length, 4.9 mm. Carapace, 2.4 mm long, 1.9 mm wide. First femur, 5.9 mm; patella and tibia, 7.3 mm; metatarsus, 7.9 mm; tarsus, 1.4 mm. Second patella and tibia, 4.4 mm; third, 1.7 mm; fourth, 2.9 mm.

Note. The male is larger than female and has a different pattern on the carapace.

Diagnosis. The epigynum is distinguished by a wide median, posterior lobe and diagonal dark streaks and round patches anteriorly (Fig. 194). The palpus is distinguished by the conductor tipped by two points visible in ventral view (Fig. 197) and an indistinctly shaped paracymbium only slightly curved in lateral view (Fig. 198).

Paratype. COLOMBIA *Dpto. Valle:* Above Saladito, 1,800 m, 20 March 1970, ♀ (W. Eberhard, MCZ).

Chrysometa lapazensis new species
Figures 199–202; Map 2

Holotype. Male from Chulumani, 1,700 m, Yungas, Dpto. La Paz, Bolivia, 17–25 Dec. 1955 (L. Peña, IRSNB). The specific name is an adjective after the locality.

Description. Male. Carapace light orange with black patch around anterior median eyes; chelicerae, labium, legs dusky, sternum orange. Dorsum of abdomen with black patches and with two lines of silver spots (Fig. 202); venter black. Eyes subequal in size. Anterior median eyes their diameter apart, slightly less than twice their diameter from laterals. Posterior median eyes their diameter apart, slightly more than twice their diameter from laterals. Clypeus height equal to diameter of anterior median eyes. Chelicerae more elongate than in other species. Total length, 2.8 mm. Carapace, 1.5 mm long, 1.1 mm wide. First femur, 2.1 mm; patella and tibia, 2.3 mm; metatarsus, 1.9 mm; tarsus, 0.8 mm. Second patella and tibia, 1.9 mm; third, 0.8 mm; fourth, 1.1 mm.

Diagnosis. The palpus is distinguished from that of other males by having a relatively small, C-shaped in ventral view, paracymbium (Fig. 199) and a heavy distal hook at the proximal end of the cymbium (Fig. 200).

Chrysometa eberhardi new species
Figures 203–208; Map 2

Holotype. Female from near Saladito, 1,700 m, Dpto. Valle, Colombia, March 1976 (W. Eberhard no. 1053, MCZ). The species is named after the collector.

Description. Female. Carapace yellow with black marks; chelicerae orange to

black; labium, endites, sternum black; legs yellow with narrow black rings. Dorsum of abdomen with white spots and black patches (Fig. 208); venter black in center with pair of white comma-shaped marks closer to spinnerets than to epigynum. Eyes subequal in size. Anterior median eyes their diameter apart, same distance from laterals. Posterior median eyes their diameter apart, 1.3 diameters from laterals. Abdomen subspherical. Total length, 4.5 mm. Carapace, 1.7 mm long, 1.2 mm wide. First femur, 2.5 mm; patella and tibia, 3.1 mm; metatarsus, 2.5 mm; tarsus, 0.9 mm. Second patella and tibia, 2.0 mm; third, 0.9 mm; fourth, 1.6 mm.

Diagnosis. This species differs from *C. cuenca* and *C. serachui* by having the median scape-like structure as wide as long in posterior view and separating the lateral plates (Fig. 207); the seminal receptacles are larger and subspherical, unlike those of related species (Figs. 203, 204).

Paratype. COLOMBIA *Dpto. Valle:* Saladito, 1,600 m, Nov. 1973, ♀ (W. Eberhard, no. 647, MCZ).

Chrysometa utcuyacu new species
Figures 209–214; Map 2

Holotype. Female from Utcuyacu, 1,600–2,200 m, Dpto. Junín, Peru, March 1948, male paratype, Feb. 1948 (F. Woytkowski, AMNH). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange with dusky V-shaped mark on thorax; chelicerae, labium, sternum dusky orange; legs orange with dark rings. Dorsum of abdomen with silver spots and dark C-shaped mark on left shoulder, mirror image on right, and posteriorly with dark band consisting of transverse bars; venter with black mark constricted posteriorly by two light patches of silver spots. Anterior lateral eyes equal to 1.5 diameters of anterior medians; posterior eyes equal to 1.3 diameters of anterior median eyes. Anterior median eyes slightly less than their diameter apart, 1.5 diameters from laterals. Posterior median eyes 0.8 diameters apart, 1.3 diameters from laterals. Abdomen oval. Total length, 6.7 mm. Carapace, 2.5 mm long, 1.9 mm wide. First femur, 4.0 mm; patella and tibia, 4.9 mm; metatarsus, 4.2 mm; tarsus, 1.2 mm. Second patella and tibia, 3.1 mm; third, 1.5 mm; fourth, 2.4 mm.

Male. Coloration similar to that of female, but with median dusky patch on thorax. Dorsum of abdomen with scattered silver spots (not continuous as in female). Eyes subequal in size. Anterior median eyes 0.8 diameters apart, slightly more than their diameter from laterals. Posterior median eyes 0.6 diameters apart, 1.2 diameters from laterals. Abdomen oval. Total length, 3.4 mm. Carapace, 1.7 mm long, 1.5 mm wide. First femur, 4.2 mm; patella and tibia, 5.2 mm; metatarsus, 5.1 mm; tarsus, 1.2 mm. Second patella and tibia, 2.6 mm; third, 1.1 mm; fourth, 2.0 mm.

Diagnosis. The epigynum is distinguished by a knob-like septum whose margins flare laterally anterior of the depressions (Fig. 211). The conductor of the male palpus, which widens distally into a diamond-shaped tip, and the complexly shaped paracymbium separate the males from others (Figs. 213, 214).

Chrysometa choroni new species
Figures 215–218; Map 2

Holotype. Female from Choroní, Est. Aragua, Venezuela, 9 March 1959 (A. M. Nadler, AMNH). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace light orange with dusky margins and dusky band from each posterior median eye touching in thoracic depression; sternum black; legs light orange with narrow dusky rings. Dorsum of abdomen with silver spots, mostly fused, absent above heart; black marks on each shoulder converging posteriorly and continuing into band of black transverse marks; sides silver; venter black with silver bands on each side approaching each other posteriorly. Eyes subequal in size. Anterior median eyes 0.8 diameters apart, their diameter from laterals. Posterior median eyes their diame-

ter apart, slightly more than their diameter from laterals. Clypeus height 0.5 diameters of anterior median eyes. Abdomen short, oval. Total length, 4.2 mm. Carapace, 1.5 mm long, 1.3 mm wide. First femur, 2.9 mm; patella and tibia, 3.1 mm; metatarsus, 2.9 mm; tarsus, 0.9 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm; fourth, 1.5 mm.

Diagnosis. The median and lateral lobes seen in ventral view of the epigynum (Fig. 217), and the distinct median swelling in posterior view (Fig. 218), distinguish this species from others.

Chrysometa cali new species
Figures 219–222; Map 2

Holotype. Female from 21 km W of Cali, Dpto. Valle, Colombia, 20 March 1955 (E. I. Schlinger, E. S. Ross, CAS). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange, head lightest; sternum, legs yellow. Abdomen with very large silver patches, no black. Eyes small, subequal in size. Anterior median eyes 1.5 diameters apart, 1.3 diameters from laterals. Posterior median eyes twice their diameter apart, 1.5 from laterals. Abdomen elongate oval (but destroyed). Total length, ca. 5 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 4.0 mm; patella and tibia, 4.5 mm; metatarsus, 4.5 mm; tarsus, 1.3 mm. Second patella and tibia, 2.9 mm; third, 1.5 mm; fourth, 2.4 mm.

Diagnosis. The epigynum of this species is distinguished by having the septum and openings only visible in posterior view (Fig. 222); in ventral view there is a pair of oval shadows (Fig. 221).

Chrysometa carmelo new species
Figures 223–230; Map 2

Holotype. Female from Quebrada La Sierrita, Serra Nueva Granada, 1,260 m, Sierra Nevada de Santa Marta, Colombia, 20 Feb. 1974 (J. A. Kochalka, MCZ). The specific name is a noun in apposition after a collecting locality.

Description. Female. Carapace orange; sternum black; legs orange gray. Dorsum of abdomen colorless, black posteriorly (Fig. 227); sides black, with two lighter patches posteriorly; venter black, no longitudinal lines. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, 2 diameters from laterals. Posterior median eyes their diameter apart, 2.5 diameters from laterals. Abdomen subspherical. Total length 3.5 mm. Carapace, 1.5 mm long, 1.1 mm wide. First femur, 1.8 mm; patella and tibia, 2.0 mm; metatarsus, 1.5 mm; tarsus, 0.7 mm. Second patella and tibia, 1.6 mm; third, 0.8 mm; fourth, 1.1 mm.

Male. Coloration like female. Eyes subequal in size. Anterior median eyes their diameter apart, 2 diameters from laterals. Posterior median eyes their diameter apart, 2.5 diameter from laterals. Clypeus height equal to four diameters of anterior median eyes. Chelicerae with a carina on side. Total length 3.0 mm. Carapace, 1.4 mm long, 1.2 mm wide. First femur, 2.0 mm; patella and tibia, 2.1 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm. Second patella and tibia, 1.7 mm; third, 0.7 mm; fourth, 1.0 mm.

Diagnosis. The epigynum of *C. carmelo* is distinguished by a triangular posterior projection containing a pair of openings (Fig. 225); the septum is narrower than that of *C. opulenta* and there are

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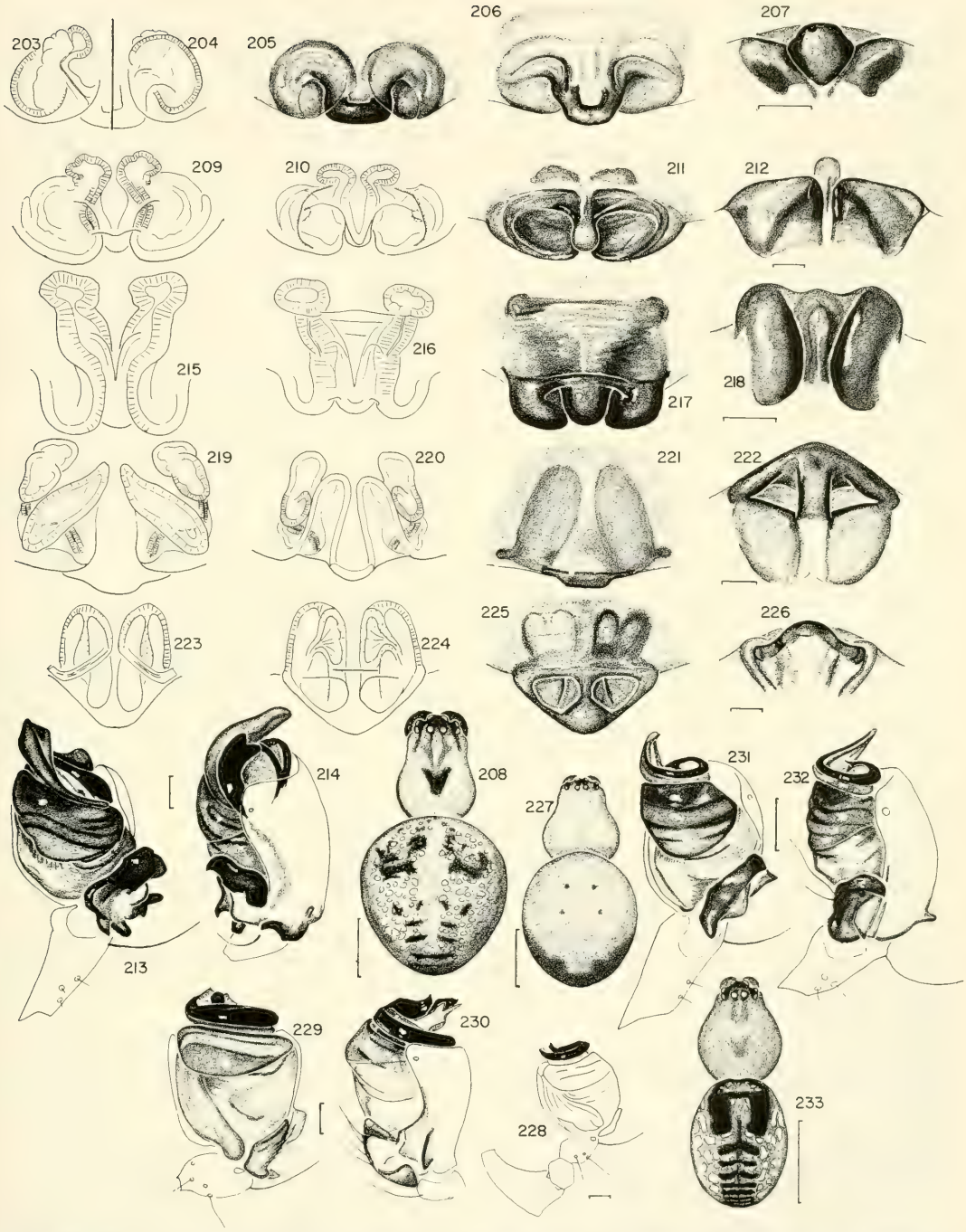
Figures 203–208. *Chrysometa eberhardi* n. sp. 203–207. Epigynum. 203. Dorsal, cleared. 204. Ventral, cleared. 205, 206. Ventral. 207. Posterior. 208. Female.

Figures 209–214. *C. utcuyacu* n. sp. 209–212. Epigynum. 209. Dorsal, cleared. 210. Ventral, cleared. 211. Ventral. 212. Posterior. 213, 214. Left male palpus. 213. Ventral. 214 Lateral.

Figures 215–218. *C. choroni* n. sp., epigynum. 215. Dorsal, cleared. 216. Ventral, cleared. 217. Ventral. 218. Posterior.

Figures 219–222. *C. cali* n. sp., epigynum. 219. Dorsal, cleared. 220. Ventral, cleared. 221. Ventral. 22. Posterior.



Figures 223–230. *C. carmelo* n. sp. 224–226. Epigynum. 224. Dorsal, cleared. 225. Ventral. 226. Posterior. 227. Female. 228–230. Male palpus. 228, 229. Ventral. 230. Lateral.

Figures 231–233. *C. aramba* n. sp. 231, 232. Male palpus. 231. Ventral. 232. Lateral. 233. Male.

Scale lines. 0.1 mm, except 208, 227, 233, 1.0 mm.

two pairs of anterior oval dark shadows (Fig. 225). The paracymbium of the male palpus is relatively small and its "lower" tip appears folded back on itself (Figs. 229, 230).

Paratype. COLOMBIA *Dpto. Magdalena:* Sierra Nevada de Santa Marta: San Pedro, Carmelo, 1,250 m, 7 Feb. 1974, ♂ (J. A. Kochalka, MCZ).

Chrysometa aramba new species
Figures 231–233; Map 2

Holotype. Male from Carambá do Sul, Est. Rio Grande do Sul, Brazil, 9 Jan. 1976 (A. Lise, MCN). The species name is an arbitrary combination of letters.

Description. Male. Carapace dusky yellow, chelicerae brown; sternum dusky brown; legs dusky yellow, ends of distal articles darker. Dorsum of abdomen with black patch on each shoulder, sides with large silver spots posteriorly with transverse black bars (Fig. 233); venter black with two parallel light streaks containing silver spots. Eyes subequal in size. Anterior median eyes 0.7 diameters apart, same distance from laterals. Posterior median eyes 0.8 diameters apart, their diameter from laterals. Abdomen oval. Total length, 2.7 mm. Carapace, 1.2 mm long, 1.0 mm wide. First femur, 2.2 mm; patella and tibia, 2.6 mm; metatarsus, 2.4 mm; tarsus, 0.7 mm. Second patella and tibia, 1.5 mm; third, 0.7 mm; fourth, 1.1 mm.

Diagnosis. This species differs from *C. boquete* by having the embolus coil of the palpus wider and the "lower" prong of the paracymbium pointed in ventral view (Figs. 231, 232).

Chrysometa yunque new species
Figures 234–240; Map 2

Holotype. Female holotype with one male, three female paratypes from El Yunque, Puerto Rico, 26 July 1931 (A. S. Mills, AMNH). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, sternum, legs dark orange. Dorsum of abdomen with a longitudinal dusky band on silver wider anterior than posterior sides straight and enclosing some silver at anterior end (Fig. 238); venter with gray pigment and silver comma-shaped marks on each side. Eyes subequal in size. Anterior median eyes their diameter apart, same distance from laterals. Posterior median eyes 0.8 diameters apart, 1.2 diameters from laterals. Abdomen subspherical (Fig. 238). Total length, 3.4 mm. Carapace, 1.3 mm long, 1.0 mm wide. First femur, 1.4 mm; patella and tibia, 1.6 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm; fourth, 0.9 mm.

Male. Coloration like female, except for scattered silver spots on abdomen. Eye sizes and placement like those of female. Abdomen subspherical. Total length, 2.3 mm. Carapace, 1.2 mm long, 0.9 mm wide. First femur, 1.5 mm; patella and tibia, 1.8 mm; metatarsus, 1.3 mm; tarsus, 0.6 mm. Second patella and tibia, 1.3 mm; third, 0.6 mm; fourth, 0.9 mm.

Diagnosis. The subtriangular median knob of the epigynum with an opening on each side (Fig. 236) distinguishes the female from other species. The short conductor, wide embolus and C-shaped in ventral view, dorsally pointing paracymbium (Figs. 239, 240) of the palpus separate the male.

Chrysometa yotoco new species
Figures 241–246; Map 3

Holotype. Female from near Yotoco, 1,600 m el., Dpto. Valle, Colombia, Dec. 1976 (W. Eberhard, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, legs orange-yellow; sternum with gray pigment on brown. Dorsum of abdomen with transverse black marks and silver spots (Fig. 246); venter black between epigynum and spinnerets, on each side a longitudinal line of silver spots. Anterior lateral eyes, posterior median eyes equal to 1.3 diameters of anterior medians; posterior laterals equal to 1.1 diameters of an-

terior medians. Anterior median eyes 0.8 diameters apart, 1.5 diameters from laterals. Posterior median eyes their diameter apart, 1.5 from laterals. Clypeus height equal to 0.4 diameters of anterior median eyes. Abdomen oval. Total length, 3.0 mm. Carapace, 1.4 mm long, 1.1 mm wide. First femur, 2.6 mm; patella and tibia, 2.8 mm; metatarsus, 2.7 mm; tarsus, 0.7 mm. Second patella and tibia, 1.6 mm; third, 0.9 mm; fourth, 1.4 mm.

Variation. Total length of females is 3.0 to 4.2 mm.

Diagnosis. The epigynum of this species differs from that of *C. boquete* by having the median septum wider than long, the lateral margins of which disappear under a transverse to round lip, which surrounds the depressions (Figs. 243, 244). In slightly posterior view round openings are visible in the depressions (Fig. 244).

Natural History, Distribution. Found 1,000 to 1,600 m, Venezuela, Colombia (Map 3).

Paratypes. VENEZUELA *Est. Aragua:* Rancho Grande, 17 Dec. 1954, ♀ (A. M. Nadler, AMNH). COLOMBIA *Dpto. Magdalena*, Sierra Nevada de Santa Marta: between Cerro Chivolo and Cerro Chumchuruba, 1,100 m, 8 March 1974, ♀ (J. Kochalka, USNM); San Pedro, June 1975, 5♀ (J. Kochalka, MCZ, AMNH, IBNA); Serra Nueva Granada, 1,500 m, 28 April 1975, 2♀ (J. Kochalka, BMNH); Valle Leumor, 1,300 m, 12 Apr. 1975, 2♀ (J. Kochalka, IBNA). *Cundinamarca:* 8 km E of El Colegio, 8 March 1955, ♀ (E. I. Schlinger, E. S. Ross, CAS).

Chrysometa obscura (Bryant), new combination
Figures 247–251; Map 2

Pseudometa obscura Bryant, 1945: 394, fig. 30, ♀. Female holotype from Pico Diego de Ocampo, North Range, 3,000–4,000 ft. [1,000–1,200 m], Dominican Republic (MCZ), examined.
Capichameta obscura:—Brignoli, 1983: 227.

Description. Female. Carapace orange-yellow, head darkest. Sternum, legs orange-yellow. Dorsum of abdomen with paired gray patches (Fig. 251). Anterior lateral eyes slightly larger than others, which are subequal in size. Anterior median eyes their diameter apart, one diameter from laterals; posterior median eyes their diameter apart, 1.5 from laterals. Abdomen subspherical. Total length, 4.0 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 2.1 mm; patella and tibia, 2.6 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 2.0 mm; third, 1.0 mm; fourth, 1.7 mm.

Diagnosis. This species differs from *C. maculata* by having the openings in transverse slits close to the posterior margin of the epigynum, and from *C. yotoco* by having a narrower septum (Fig. 249).

Chrysometa conspersa (Bryant), new combination
Figures 252–256; Map 2

Pseudometa conspersa Bryant, 1945: 391, fig. 29, ♀. Female holotype from La Visité, Haiti, 6,000–7,000 ft. [2,000–2,300 m] (MCZ), examined.
Capichameta conspersa:—Brignoli, 1983: 227.

Description. Female. Carapace orange-yellow, head darker in middle. Sternum yellow, gray on sides. Legs yellow with narrow dark rings, more distinct on underside. Dorsum of abdomen with black and white spots, posteriorly with transverse bars (Fig. 256). Sides dark, maculated. Venter with square black patch between epigynum and spinnerets. Anterior lateral eyes 1.2 diameters of anterior medians; posterior median eyes 1.2 diameters; posterior lateral eyes 0.9 diameters. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes slightly less than their diameter apart, 1.5 diameters from laterals. Abdomen oval. Total length, 4.5 mm. Carapace, 2.2 mm long, 1.7 mm wide. First femur, 4.2 mm; patella and tibia, 3.2 mm; metatarsus, 3.0 mm; tarsus, 1.3 mm. Second patella and tibia, 2.9 mm; third, 1.4 mm; fourth, 2.2 mm.

Diagnosis. This species is distinguished

by having the septum and transverse bar framed by a semicircular lip (Fig. 254).

Chrysometa magdalena new species
Figures 257–261; Map 2

Holotype. Female holotype and male paratype from Serra Nueva Granada, 1,900 m, Sierra Nevada de Santa Marta, Dpto. Magdalena, Colombia, 7 April 1975 (J. A. Kochalka, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, coxae yellowish white; sternum greenish gray, legs gray. Dorsum of abdomen purplish white with silver spots, black posteriorly on sides (Fig. 261); sides ventrally dark gray; venter gray with median black patch, no longitudinal lines. Carapace high and rounded. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, three diameters from laterals. Posterior median eyes slightly more than their diameter apart, 2.5 their diameter from laterals. Clypeus height equal to 1.7 diameters of anterior median eyes. Abdomen subspherical. Total length, 3.4 mm. Carapace, 1.3 mm long, 1.1 mm wide. First femur, 1.9 mm; patella and tibia, 2.3 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm. Second patella and tibia, 1.8 mm; third, 0.9 mm; fourth 1.2 mm.

Diagnosis. The posteriorly extending lobe of the epigynum with the openings in a groove on each side (Fig. 259) separates this species from other *Chrysometa.*

Chrysometa huila new species
Figures 262–268; Map 3

Holotype. Male from Finca Meremberg, 10 km E Santa Leticia, 2,300 m el., Dpto. Huila, Colombia, March 1979 (W. Eberhard, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, legs orange-yellow; sternum black. Dorsum of abdomen with silver spots, smaller ones posteriorly; black in midline (Fig. 266). Venter black with line of silver pigment spots on each side. Anterior lateral eyes, posterior median eyes 1.2 diameters of anterior median eyes; posterior laterals equal to diameter of anterior median eyes. Anterior median eyes their diameter apart, 1.3 diameters from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Abdomen elongate oval (Fig. 266). Total length, 4.5 mm. Carapace, 1.8 mm long, 1.4 mm wide. First femur, 2.5 mm; patella and tibia, 3.1 mm; metatarsus, 2.5 mm; tarsus, 1.1 mm. Second patella and tibia, 2.0 mm; third, 1.1 mm; fourth, 1.6 mm.

Male. Carapace yellow, head region orange. Sternum, legs yellow. Dorsum and sides of abdomen with large silver patches, posterior with ten fine gray transverse bars; venter gray around spinnerets, and with two longitudinal rows of silver spots. Anterior lateral, posterior median eyes equal to diameter of anterior median eyes; posterior lateral eyes 0.8 diameters of anterior medians. Anterior median eyes their diameter apart, slightly more than their diameter from laterals. Posterior median eyes 0.8 diameters apart, 1.2 diameters from laterals. Abdomen oval. Total length, 3.5 mm. Carapace, 1.7 mm long, 1.4 mm wide. First femur, 4.0 mm; patella and tibia, 4.9 mm; metatarsus, 5.3 mm; tarsus, 1.3 mm. Second patella and tibia, 2.7 mm; third, 1.2 mm; fourth, 1.9 mm.

Note. Both depressions of the epigynum are plugged with irremovable exudate.

Diagnosis. Females differ by having the

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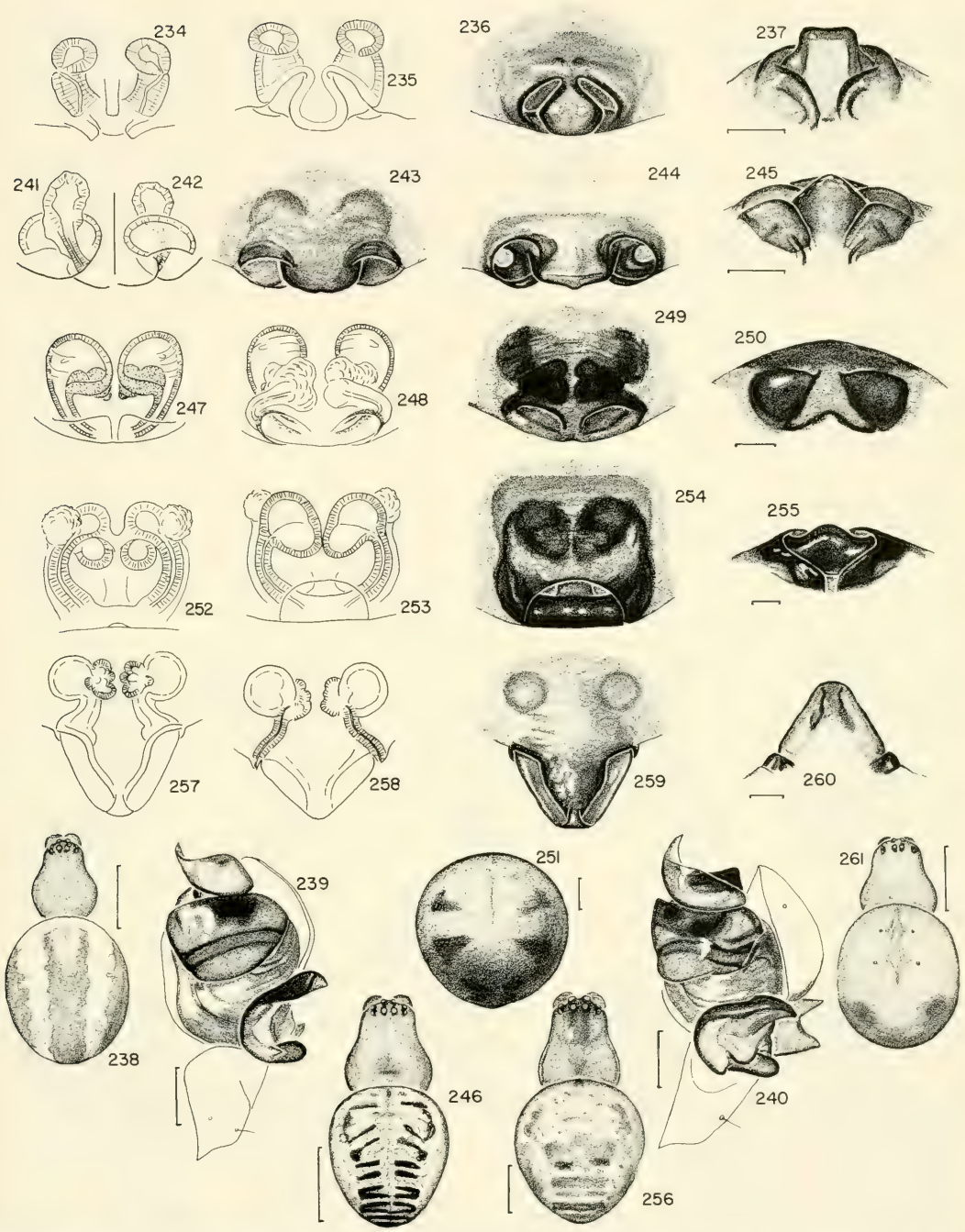
Figures 234–240. *Chrysometa yunque* n. sp. 234–237. Epigynum. 234. Dorsal, cleared. 235. Ventral, cleared. 236. Ventral. 237. Posterior. 238. Female. 239, 240. Left male palpus. 239. Ventral. 240. Lateral.

Figures 241–246. *C. yotoco* n. sp. 241–245. Epigynum. 241. Dorsal, cleared. 242. Ventral, cleared. 243, 244. Ventral. 245. Posterior. 246. Female.

Figures 247–251. *C. obscura* (Bryant). 247–250. Epigynum. 247. Dorsal, cleared. 248. Ventral, cleared. 249. Ventral. 250. Posterior. 251. Female abdomen, dorsal.



Figures 252–256. *C. conspersa* (Bryant). 252–255. Epigynum. 252. Dorsal, cleared. 253. Ventral, cleared. 254. Ventral. 255. Posterior. 256. Female.

Figures 257–261. *C. magdalena* n. sp. 257–260. Epigynum. 257. Dorsal, cleared. 258. Ventral, cleared. 259. Ventral. 260. Posterior. 261. Female.

Scale lines. 0.1 mm, except Figures 238, 246, 251, 256, 261, 1.0 mm.

central depression of the epigynum divided by a median anterior lobe and lacking an anterior transverse bar (Fig. 264). Males can be separated by having a three-pointed paracymbium, cog-wheel-shaped in lateral view (Figs. 267, 268).

Natural History, Distribution. From 2,300 m, southern Colombia and northern Ecuador (Map 3).

Paratypes. COLOMBIA *Dpto. Huila:* 19 km E of Santa Leticia, 2,300 m el., March 1976, ♀ (W. Eberhard, MCZ). ECUADOR *Prov. Carchi:* Troya, 2,900–2,950 m, 10–13 June 1965, 2♀ (L. Peña, MCZ).

Chrysometa penai new species
Figures 269–273; Map 3

Holotype. Female from Cord. Tinajillas, 3,100 m [south of Cuenca, Prov. Azuay], Ecuador, 18–21 March 1965 (L. Peña, MCZ). The species is named after the collector.

Description. Female. Carapace gray-orange; sternum black; coxae yellow; legs orange-gray. Dorsum of abdomen with silver platelets separated by cracks, black shoulders and gray transverse posterior marks (Fig. 273). Sides silver; venter black between epigynum and spinnerets, silver longitudinal band on each side. Secondary eyes equal to 1.3 diameters of anterior medians. Anterior median eyes slightly more than their diameter apart, 1.6 diameters from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Abdomen oval (but specimen shriveled). Total length, 4.7 mm. Carapace, 1.8 mm long, 1.5 mm wide. First femur, 2.5 mm; patella and tibia, 2.8 mm; metatarsus, 2.3 mm; tarsus, 0.9 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm; fourth, 1.5 mm.

Diagnosis. This species differs from *C. pilimbala* by having the depression of the epigynum twice as wide as long (Fig. 271).

Paratype. ECUADOR *Prov. Pichincha:* Quito, paramo, 3,400 m, 25 April 1942, 2♀ (H. Frizzell, O. L. Haught, EPC).

Chrysometa pilimbala new species
Figures 274–280; Map 3

Holotype. Female holotype with 14 female, 4 male paratypes from Parque Nacional Puracé, path from Pilimbalá to Volcán Puracé, 3,690 m, 12–13 Jan. 1943, Dpto. Cauca, Colombia (J. A. Kochalka, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace grayish yellow, middle darker; sternum black; legs ringed. Dorsum of abdomen with silver spots covered by a black longitudinal median band, widest anteriorly; cardiac area without black pigment. Sides gray on silver spots; venter black with a longitudinal line of silver spots on each side. Lateral eyes equal to 1.3 diameters of anterior median eyes; posterior median eyes 1.5 diameters of anterior median eyes. Anterior median eyes slightly more than their diameter apart, 1.8 diameters from laterals. Posterior median eyes 0.8 diameters apart, 1.3 diameters from laterals. Abdomen oval. Total length, 5.2 mm. Cara-

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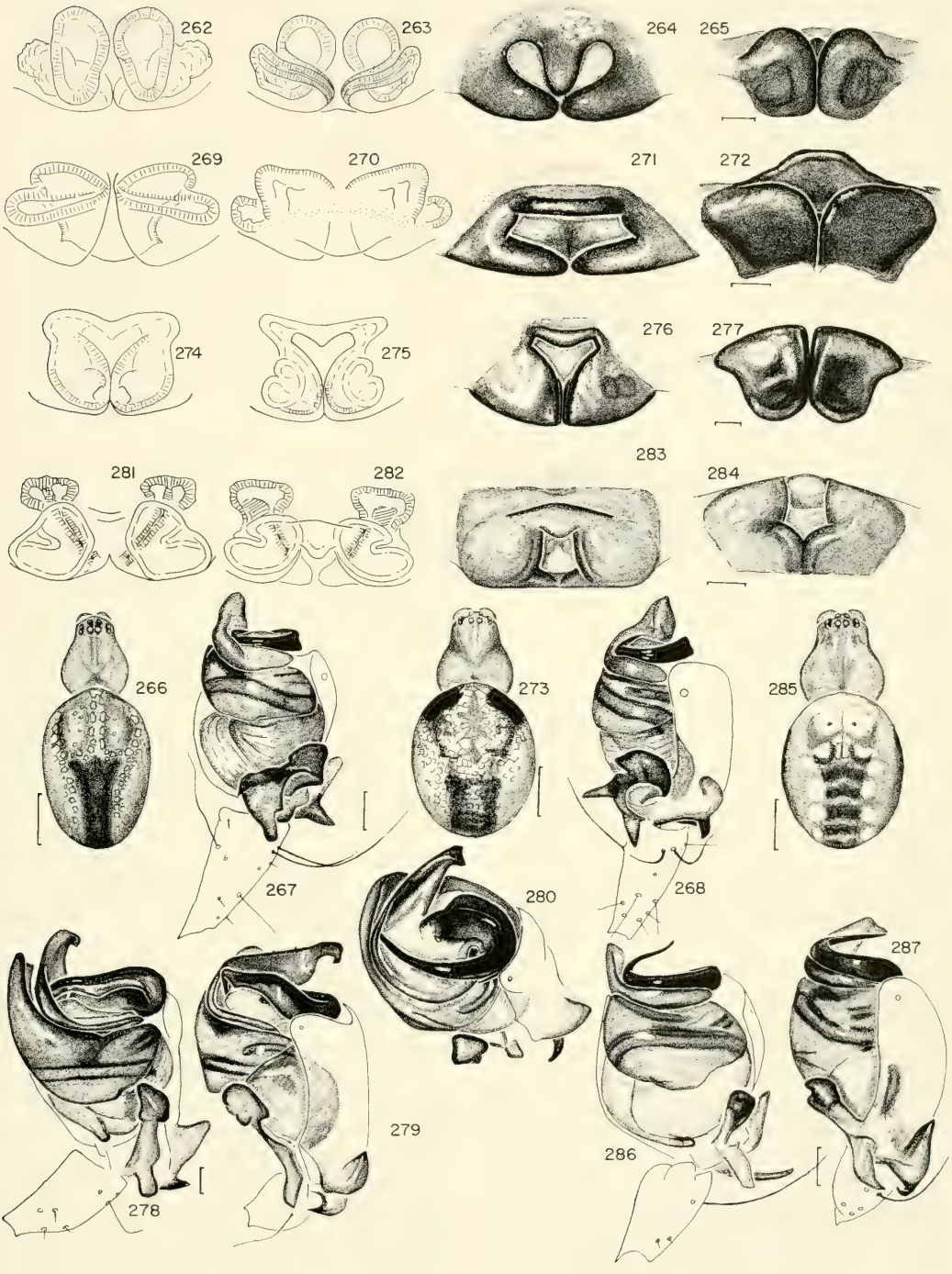
Figures 262–268. *Chrysometa huila* n. sp. 262–265. Epigynum. 262. Dorsal, cleared. 263. Ventral, cleared. 264. Ventral. 265. Posterior. 266. Female. 267, 268. Left male palpus. 267. Ventral. 268. Lateral.

Figures 269–273. *C. penai* n. sp. 269–272. Epigynum. 269. Dorsal, cleared. 270. Ventral, cleared. 271. Ventral. 272. Posterior. 273. Female.

Figures 274–280. *C. pilimbala* n. sp. 274–277. Epigynum. 274. Dorsal, cleared. 275. Ventral, cleared. 276. Ventral. 277. Posterior. 278–280. Male palpus. 278. Ventral. 279. Lateral. 280. Apical.

Figures 281–287. *C. kochalkai* n. sp. 281–284. Epigynum. 281. Dorsal, cleared. 282. Ventral, cleared. 283. Ventral. 284. Posterior. 285. Female. 286, 287. Male palpus. 286. Ventral. 287. Lateral.

Scale lines. 0.1 mm, except Figures 266, 273, 285, 1.0 mm.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pace, 2.0 mm long, 1.5 mm wide. First femur, 2.5 mm; patella and tibia, 3.0 mm; metatarsus, 2.3 mm; tarsus, 1.0 mm. Second patella and tibia, 2.0 mm; third, 1.1 mm; fourth, 1.6 mm.

Male. Coloration like female. Abdomen with less black pigment, but with indistinct posterodorsal transverse marks. Eyes subequal in size. Anterior median eyes their diameter apart, 1.2 diameters from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Abdomen oval. Total length, 4.4 mm. Carapace, 2.1 mm long, 1.6 mm wide. First femur, 3.1 mm; patella and tibia, 3.9 mm; metatarsus, 3.5 mm; tarsus, 1.2 mm. Second patella and tibia, 2.3 mm; third, 1.2 mm; fourth, 1.7 mm.

Diagnosis. Females differ from *C. penai* and *C. kochalkai* by having the depression of the epigynum subtriangular and as wide as long (Fig. 276). The male can be separated from others by the stalked paracymbium and by the small distal hook of the conductor of the palpus (Figs. 278, 279).

Paratypes. Deposited as follows: ♀, ♂ MCZ; ♀ AMNH; ♀, ♂ USNM; ♀, ♂ BMNH; 10♀, ♂ IBNA.

Chrysometa kochalkai new species
Figures 281–287; Map 3

Holotype. Female holotype with two male, four female paratypes from Río Donachui, timberline, 4,000 m, Sierra Nevada de Santa Marta, Colombia, 18 Jan. 1974 (J. A. Kochalka, MCZ). This species is named after the collector.

Description. Female. Carapace yellow-white with black marks; sternum black; legs with narrow black rings. Dorsum of abdomen with usual black markings and posterior longitudinal black band, no silver spots (Fig. 285). Secondary eyes equal to 1.2 diameters of anterior medians. Anterior median eyes 1.2 diameters apart, same distance from laterals. Posterior median eyes slightly less than their diameter apart, 1.5 diameters from laterals. Abdomen oval. Total length, 4.5 mm. Carapace, 1.8 mm long, 1.5 mm wide. First femur, 2.5 mm; patella and tibia, 3.1 mm; metatarsus, 2.5 mm; tarsus, 1.1 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.7 mm.

Male. Coloration like female. Secondary eyes equal to 1.3 diameters of anterior median eyes. Anterior median eyes their diameter apart, 1.5 diameters from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Total length, 3.7 mm. Carapace, 1.6 mm long, 1.3 mm wide. First femur, 2.8 mm; patella and tibia, 3.6 mm; metatarsus, 3.4 mm; tarsus, 1.1 mm. Second patella and tibia, 2.1 mm; third, 1.0 mm; fourth, 1.6 mm.

Diagnosis. The epigynum differs from that of *C. pilimbala* and *C. penai* by having a square-shaped depression (Fig. 283). Males differ from related species by the relatively short "upper" stalk of the paracymbium and the slender embolus of the palpus (Figs. 286, 287).

Records. COLOMBIA *Dpto. Magdalena*, Sierra Nevada de Santa Marta: Río Donachui, 3,800 m, 5 Jan. 1974, ♀, imm., 3,600 m, 2 Jan. 1973, 6♀, 8 imm. (J. Kochalka, IBNA, AMNH, BMNH, USNM).

Chrysometa satura new species
Figures 288–292; Map 3

Holotype. Female from Cerro de La Muerte, Cartago Prov., Costa Rica, 9 Aug. 1983 (J. Coddington, MCZ). The specific name is an arbitrary combination of letters.

Description. Female. Carapace yellow with black pattern. Sternum black; legs ringed black on yellow. Dorsum of abdomen black with gray and silver marks (Fig. 292); venter black with longitudinal line of silver spots on each side. Eyes subequal in size. Anterior median eyes their diameter apart, 1.3 diameters from laterals. Posterior median eyes their diameter apart, 1.7 diameters from laterals. Abdomen oval. Total length, 4.5 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 2.5 mm; patella and tibia, 3.1 mm;

metatarsus, 2.5 mm; tarsus, 1.0 mm. Second patella and tibia, 1.9 mm; third, 1.1 mm; fourth, 1.2 mm.

Diagnosis. The epigynum of this species differs by being heavily sclerotized with a transverse anterior bar lacking a posterior lip, and by the two comma-shaped openings separated by a narrow septum (Fig. 290).

Chrysometa bella (Banks), new combination
Figures 293–300; Map 3

Pseudometa bella Banks, 1909: 208, pl. 6, fig. 30, ♂. Male holotype from Santa María, Prov. San José, Costa Rica (MCZ), examined. Roewer, 1942: 922. Bonnet, 1957: 3817.

Description. Female. Carapace orange-yellow with longitudinal gray band. Sternum black; legs ringed. Dorsum of abdomen with silver spots, anteriorly with pairs of transverse bars, posteriorly with a black folium (Fig. 297); venter black between epigynum and spinnerets, with longitudinal white line on each side. Anterior lateral eyes, posterior median eyes 1.2 diameters of anterior median eyes; posterior lateral eyes equal to diameter of anterior medians. Anterior median eyes slightly more than their diameter apart, 1.2 diameters from laterals. Posterior median eyes slightly less than their diameter apart, 1.5 diameters from laterals. Abdomen oval. Total length, 5.3 mm. Carapace, 2.4 mm long, 1.7 mm wide. First femur, 3.2 mm; patella and tibia, 3.8 mm; metatarsus, 3.2 mm; tarsus, 1.2 mm. Second patella and tibia, 2.6 mm; third, 1.3 mm; fourth, 1.9 mm.

Male. Carapace orange with darker patches and light median line; sternum black; legs light yellow. Dorsum of abdomen with gray anteriorly, in middle a pair of white patches, posterior with a black longitudinal band, sides silvery dorsally; venter black with pair of longitudinal white lines. Lateral eyes equal to 1.2 diameters of anterior median eyes; posterior median eyes equal to 1.3 diameters of anterior median eyes. Anterior median eyes slightly more than their diameter apart, 1.3 diameters from laterals. Posterior median eyes slightly less than their diameter apart, 1.2 diameters from laterals. Total length, 3.8 mm. Carapace, 2.0 mm long, 1.3 mm wide. First femur, 3.9 mm; patella and tibia, 4.5 mm; metatarsus, 4.8 mm; tarsus, 1.3 mm. Second patella and tibia, 2.5 mm; third, 1.1 mm; fourth, 2.0 mm.

Note. Male and female have not been collected together but have been matched because of their similarity. There is the possibility that the female of *C. satura* belongs with the male *C. bella.*

Diagnosis. The female epigynum differs from that of *C. satura* and *C. pichincha* by the more distinct posteriorly pointing transverse bar and by the oblique openings separated by more than their length (Fig. 295). The short biforked embolus, one fork being the terminal apophysis, separates the male from others with a stalked paracymbium (Figs. 298–300).

Record. COSTA RICA *Prov. Cartago:* Cerro de la Muerte, 18 Feb. 1979, ♀ (J. Coddington, MCZ).

Chrysometa pichincha new species
Figures 301–304; Map 3

Holotype. Female from road between Quito and Santo Domingo, 2,300–2,400 m, Prov. Pichincha, Ecuador, 13–25 Feb. 1965 (L. Peña, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, legs orange; labium, sternum black. Dorsum of abdomen with silver spots less than their diameter apart, longitudinal band wider anteriorly than posteriorly, sides of band parallel posteriorly and with dark patches and silver spots in center. Sides of abdomen with silver patches; venter black with a longitudinal silver line on each side. Anterior lateral eyes equal to 1.3 diameters of anterior medians; posterior eyes equal to 1.8 diameters of anterior median eyes. Anterior median eyes 1.5 diameters apart,

3 from laterals. Posterior median eyes their diameter apart, 2 from laterals. Abdomen elongate oval. Total length, 5.4 mm. Carapace, 2.0 mm long, 1.6 mm wide. First femur, 2.8 mm; patella and tibia, 3.6 mm; metatarsus, 3.6 mm; tarsus, 1.1 mm. Second patella and tibia, 2.5 mm; third, 1.3 mm; fourth, 1.9 mm.

Diagnosis. The straight transverse bar of the epigynum separates *C. pichincha* from *C. bella*, as do the openings, which are much further apart in *C. pichincha* (Fig. 303).

Chrysometa ecarup new species
Figures 305–309; Map 3

Holotype. Female holotype and two female paratypes from Puracé Natl. Park, path from Pilimbalá to Volcán Puracé, 3,690 m, Colombia, 12–13 Jan. 1983 (J. Kochalka, MCZ). The specific name is an anagram of the locality.

Description. Carapace yellow with black marks; sternum black. Dorsum of abdomen black anteriorly, posteriorly with black folium; venter black with a light line on each side containing silver spots. Secondary eyes equal to 1.3 diameters of anterior medians. Anterior median eyes their diameter apart, slightly more than their diameter from laterals. Posterior median eyes 0.8 diameters apart, 1.2 diameters from laterals. Abdomen shield-shaped (Fig. 309) with two humps. Total length, 4.4 mm. Carapace, 1.8 mm long, 1.4 mm wide. First femur, 2.7 mm; patella and tibia, 3.2 mm; metatarsus, 2.7 mm; tarsus, 1.1 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.7 mm.

Diagnosis. This species differs from *C. pichincha* and *C. bella* by having the openings of the epigynum hidden under the transverse bar (Fig. 307).

Chrysometa zelotypa (Keyserling), new combination
Figures 310–333; Map 3

Epeira zelotypa Keyserling, 1883: 202, pl. 15, fig. 7, ♀. Female holotype from San Mateo [Dpto. Lima], Peru, 3,000 m (PAN), examined; two juvenile paratypes, one in BMNH. Keyserling, 1893, 4: 141, pl. 7, fig. 104, ♀.

Meta alticola Berland, 1913: 90, pl. 8, figs. 31–35, ♂, ♀. Seven female syntypes from Casitagua [Cerro Casitagua, 0°2′S, 78°29′W], male from Tulcán [Carchi Prov.], Ecuador, lost. Roewer, 1942: 918. Bonnet, 1957: 2785. NEW SYNONYMY.

Aranea zelotypa:—Roewer, 1942: 857.

Araneus zelotypus:—Bonnet, 1957: 632.

Note. Berland's illustrations of the palpus (figs. 33, 34) place the male in this species; the female may be another species.

Description. Female type of *E. zelotypa.* Carapace with fine median light line, border of carapace lighter brown, with pigment streaking from center towards sides. Sternum dark brown, coxae light; legs with fine dark rings on light. Dorsum of abdomen with dark folium, scattered white pigment spots to sides of folium, black on shoulders (Figs. 325, 327); venter with two white lines, intermediate area black, enclosing some white spots posteriorly (Fig. 326). Secondary eyes slightly larger than anterior medians. Anterior median eyes their diameter apart, 1.2 diameters from laterals. Posterior median eyes 0.8 diameters apart, their diameter from laterals. Abdomen triangular with pair of anterior humps. Total length, 4.0 mm. Carapace, 1.7 mm long, 1.4 mm wide. First femur, 2.6 mm; patella and tibia, 2.9 mm; metatarsus, 2.3 mm; tarsus, 1.0 mm. Second patella and tibia, 1.9 mm; third, 0.9 mm; fourth, 1.6 mm.

Male. Coloration like female. Eyes subequal in size. Anterior median eyes slight-

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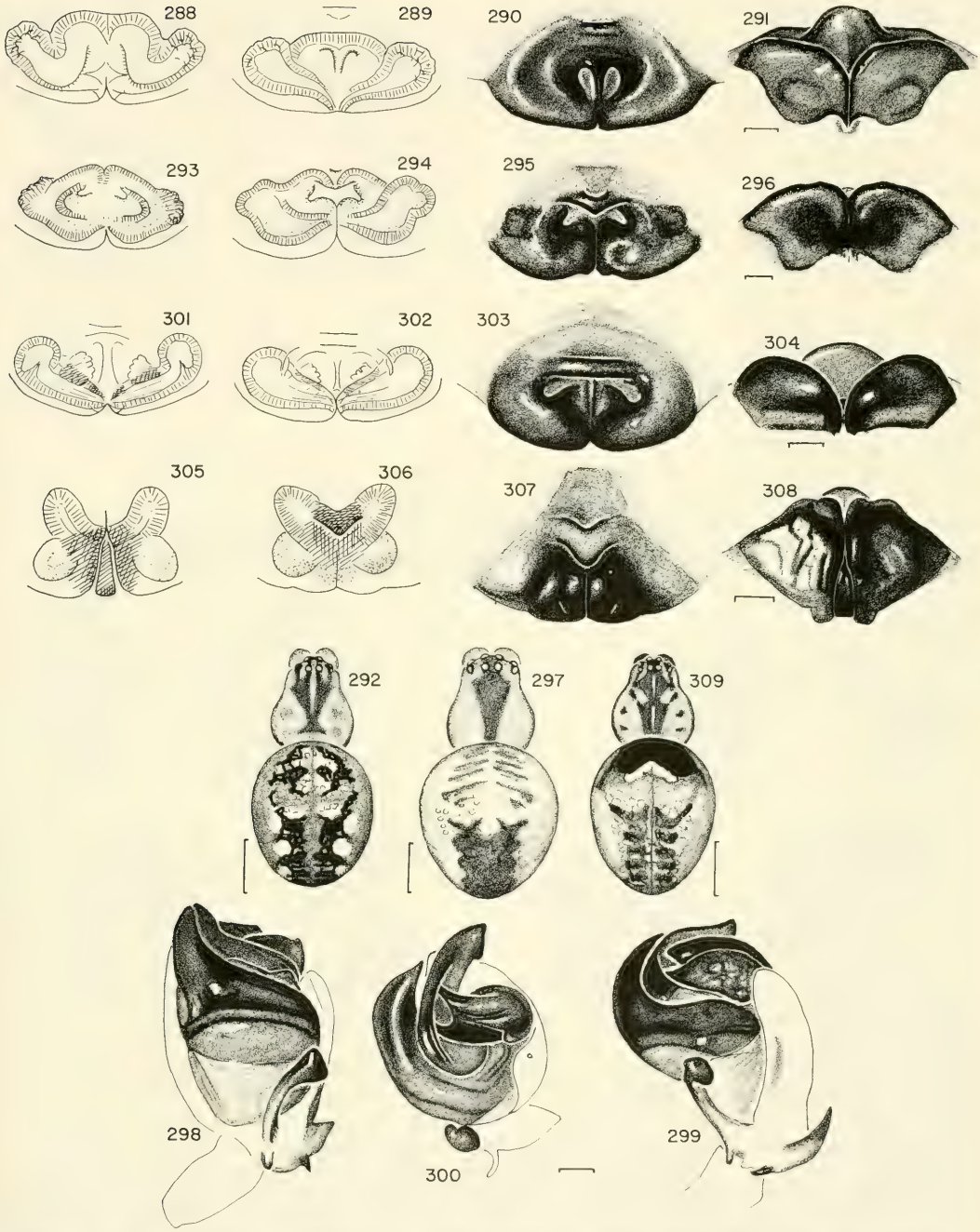
Figures 288–292. *Chrysometa satura* n. sp. 288–291. Epigynum. 288. Dorsal, cleared. 289. Ventral, cleared. 290. Ventral. 291. Posterior. 292. Female.

Figures 293–300. *C. bella* (Banks). 293–296. Epigynum. 293. Posterior, cleared. 294. Ventral, cleared. 295. Ventral. 296. Posterior. 297. Female. 298–300. Left male palpus. 298. Ventral. 299. Lateral. 300. Apical.



Figures 301–304. *C. pichincha* n. sp., epigynum. 301. Dorsal, cleared. 302. Ventral, cleared. 303. Ventral. 304. Posterior.

Figures 305–309. *C. ecarup* n. sp. 305–308. Epigynum. 305. Dorsal, cleared. 306. Ventral, cleared. 307. Ventral. 308. Posterior. 309. Female.

Scale lines. 0.1 mm, except Figures 292, 297, 309, 1.0 mm.

ly more than their diameter apart, 1.5 diameters from laterals. Posterior median eyes slightly more than their diameter apart, 1.5 diameters from laterals. Total length, 4.2 mm. Carapace, 2.1 mm long, 1.7 mm wide. First femur, 4.4 mm; patella and tibia, 5.3 mm; metatarsus, 5.8 mm; tarsus, 1.5 mm. Second patella and tibia, 2.8 mm; third, 1.3 mm, fourth, 2.1 mm.

Variation. Specimens from no two localities are alike. Males vary in the genitalia (Figs. 328–333); all were at first considered different species. The few males available and the differences in paracymbium shape (Figs. 329, 332) suggest that this may indeed be so. The type specimen of *zelotypa* has a short abdomen with humps (Fig. 327), while all other females had an oval abdomen (Fig. 325). Females varied in total length from 3.5 to 5.1 mm.

Diagnosis. The female epigynum differs from similar species by the large oval depression sometimes containing a median swelling or ridge and by having a transverse bar or lobe anterior to the depression (Figs. 312, 316, 320, 323). The male palpus has a stalked paracymbium, the conductor is widened at its base and the base of the embolus and terminal apophysis has a wide pointed lobe (Figs. 328–333).

Natural History, Distribution. Found at high elevations 2,400 to 3,500 m, Costa Rica, Venezuela to Peru (Map 3).

Records. COSTA RICA *Prov. Heredia:* Volcán Poás, summit 2,400 m, 28 June 1979, ♀ (J. Coddington, USNM). *Cartago:* Volcán Irazú, 2,400 m, 6 Aug. 1963, ♀ (W. Peck, EPC), 3,400 m, 26 Nov. 1955, ♀ (B. Malkin, AMNH); Cerro de la Muerte, 30 July 1980, ♀ (J. Coddington, MCZ). PANAMA *Prov. Chiriquí:* Cerro Punta near Guadalupe, 2,500 m, 25 Oct. 1983, ♀ (Y. D. Lubin, MCZ). VENEZUELA *Est. Mérida:* Paramo Mucubaji, 3,400 m, on Highway 1, 3 km from intersection of Highway 7, 13 Jan. 1985, ♀ (J. Palmer, MCZ). COLOMBIA *Dpto. Nariño:* 26 km east of Santiago, 3 March 1955, ♀ (E. I. Schlinger, E. S. Ross, CAS). ECUADOR *Prov. Carchi:* Volcán Chiles, 2,000–3,100 m, 26, 27 June 1965, ♀ (L. Peña, MCZ); Troya, 2,900–2,950 m, 10, 13 June 1965, 2♀, 2♂ (L. Peña, MCZ); *Pichincha:* Quito, Santo Domingo Rd., 2,500 m, 25 Apr. 1942, 2♀, nr. Quito, paramo, 3,400 m, 25 Apr. 1942, 2♀, 2 imm. (O. L. Haught, H. E. Frizzell, EPC). *Napo*: E of Papallacta, 6–8 Oct. 1977, 10♀, 3♂, 7 imm. (L. Peña, AMNH). *Tungurahua:* Minza Chica, paramo, 3,500 m, April 1939, 2♀ (F. M. Brown, AMNH). *Bolívar:* Hda. Talahua, 3,100 m, 29 Apr. 1939, ♀ (F. M. Brown, AMNH).

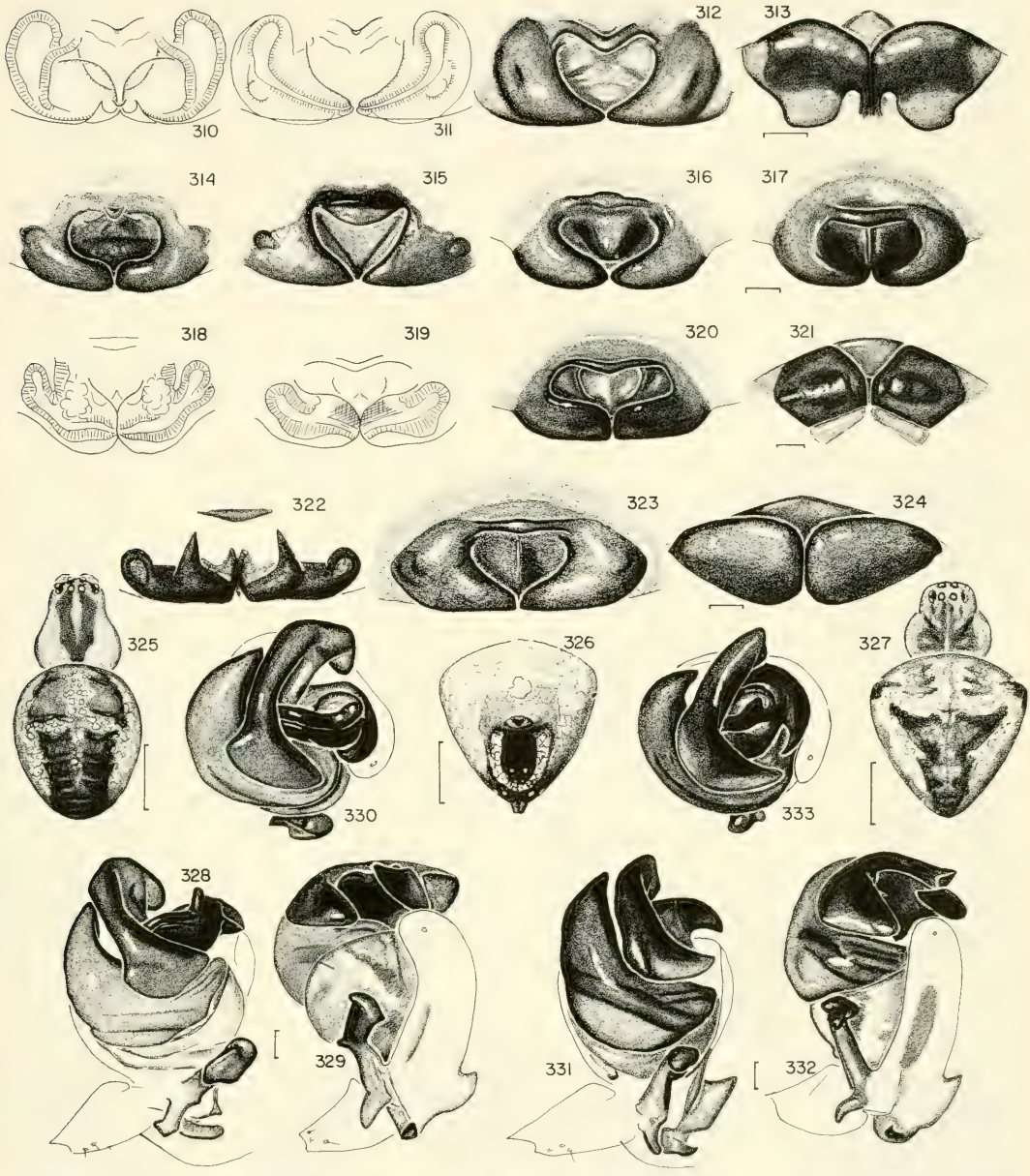
Chrysometa bigibbosa (Keyserling), new combination
Figures 334–340; Map 3

Tetragnatha bigibbosa Keyserling, 1863: 144, pl. 7, figs. 1, 2, ♀. Female holotype from Bogotá, Colombia (BMNH), examined.

Argyroepeira bigibbosa:—Keyserling, 1893: 330, pl. 17, fig. 244, ♀.

Leucauge bigibbosa:—Petrunkevitch, 1930: 273. Roewer, 1942: 1009. Bonnet, 1957: 2463.

Description. Female. Carapace yellowish white with median white pigment patch and two pairs of dark spots on thorax. Sternum brown, maculated, with median white pigment patch; legs yellowish. Dorsum of abdomen with large and small white pigment spots, arranged in distinctive pattern (Fig. 338); sides with white pigment spots; venter with two lateral longitudinal bands of large white pigment spots in between smaller pigment spots (Fig. 339); dark pigment surrounding white patches posteriorly on venter and on sides of humps. Eyes subequal in size. Anterior median eyes 1.4 diameters apart, 2.4 diameters from laterals. Posterior median eyes 1.4 diameters apart, 2.4 diameters from laterals. Abdomen oval with two slender tubercles (Figs. 338, 340). Total length, 6.8 mm. Carapace, 3.0 mm long, 2.3 mm wide. First femur, 5.5 mm; patella and tibia, 6.8 mm; metatarsus, 6.3



Figures 310–333. *Chrysometa zelotypa* (Keyserling). 310–324. Epigynum. 310, 318, 322. Dorsal, cleared. 311, 319. Ventral, cleared. 312, 314–317, 320, 323. Venter. 313, 321, 324. Posterior. 310–313. (Panama). 314. (Costa Rica). 315. (Venezuela). 316. (Prov. Carchi, Ecuador). 318–321 (Quito, Ecuador). 322–324. (Holotype, Peru). 325–327. Female. 326. Abdomen, ventral. 325. (Panama). 326, 327. (Holotype, Peru). 328–333. Male left palpus. 328, 331. Ventral. 329, 332. Lateral. 330, 333. Apical. 328–330. (Prov. Carchi, Ecuador). 331–333. (Prov. Napo, Ecuador).

Scale lines. 0.1 mm, except Figures 325–327, 1.0 mm.

mm; tarsus, 1.8 mm. Second patella and tibia, 4.3 mm; third, 2.4 mm; fourth 3.8 mm.

Diagnosis. The species differs from *C. explorans* by having anterior tubercles on the abdomen (Figs. 338, 340) and the epigynum with a wider scape and depressions (Fig. 336).

Chrysometa explorans (Chamberlin), new combination
Figures 341–345; Map 3

Meta explorans Chamberlin, 1916: 242, pl. 18, fig. 5, ♀. Female holotype from Conservidayo River [Conservidayoc, Dpto. Cuzco], Peru (MCZ), examined. Roewer, 1942: 918. Bonnet, 1957: 2786.

Description. Female. Carapace orange with lighter dorsal mark. Labium, sternum black; legs orange. Dorsum of abdomen with white pigment spots, posteriorly with a darker longitudinal band containing darker spots (Fig. 345); venter gray with parallel white lines. Anterior lateral eyes 1.5 diameters of anterior medians; posterior median eyes 1.5 diameters, posterior laterals equal to diameter of anterior medians. Anterior median eyes slightly more than their diameter apart, 1.8 diameters from laterals. Posterior median eyes their diameter apart, 1.9 from laterals. Abdomen oval with small humps. Total length, 5.5 mm. Carapace, 2.2 mm long, 1.7 mm wide. First femur, 2.7 mm; patella and tibia, 3.5 mm; metatarsus, 2.9 mm; tarsus, 1.2 mm. Second patella and tibia, 2.5 mm; third, 1.2 mm; fourth, 1.9 mm.

Note. It is possible that these specimens belong to *C. bigibbosa*.

Diagnosis. This species differs from *C. bigibbosa* by having only indistinct humps on the abdomen (Fig. 345) and having the epigynum with a narrower scape and depressions (Fig. 343).

Records. PERU *Dpto. Cuzco:* Cuzco, 3,300 m, Aug. 1965, ♀ (P. Wygodzinsky, AMNH); Tincochaca, 2,300 m, Aug. 1911, ♀ (Yale Peruv. Exped., MCZ); Urubamba, 3,100 m, July 1911, ♀ (Yale Peruv. Exped., MCZ).

Chrysometa macintyrei new species
Figures 346–350; Map 3

Holotype. Female from Prov. Tungurahua, 2,600 m, Ecuador, 6 May 1939 (W. Clarke-Macintyre, AMNH). The species is named after the collector.

Description. Female. Carapace dark orange; sternum brown; legs dark orange. Dorsum of abdomen with tiny silver spots and pair of black marks; sides with silver spots (Fig. 350); venter with dusky rectangular mark in center, with line of silver spots on each side, sides with silver spots. Secondary eyes equal to 1.3 diameters of anterior median eyes. Anterior median eyes their diameter apart, 1.5 diameters from laterals. Posterior median eyes their diameter apart, slightly more than their

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Figures 334–340. *Chrysometa bigibbosa* (Keyserling). 334–337. Epigynum. 334. Dorsal, cleared. 335. Ventral, cleared. 336. Ventral. 337. Posterior. 338–340. Female. 339, 340. Abdomen. 339. Ventral. 340. Lateral.

Figures 341–345. *C. explorans* (Chamberlin). 341–344. Epigynum. 341. Dorsal, cleared. 342. Ventral, cleared. 343. Ventral. 344. Posterior. 345. Female.

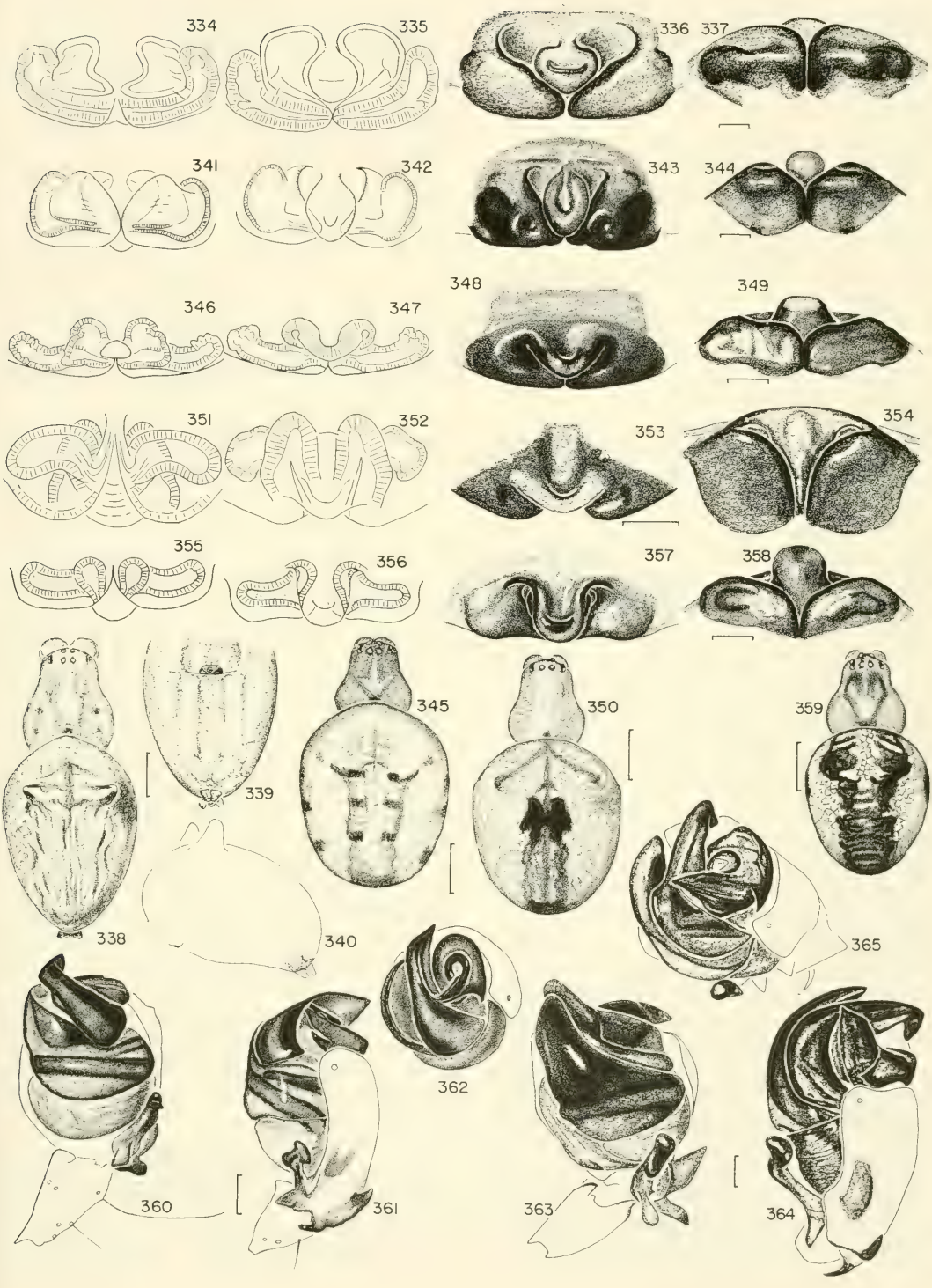
Figures 346–350. *C. macintyrei* n. sp. 346–349. Epigynum. 346. Dorsal, cleared. 347. Ventral, cleared. 348. Ventral. 349. Posterior. 350. Female.

Figures 351–354. *C. bolivari* n. sp., epigynum. 351. Dorsal, cleared. 352. Ventral, cleared. 353. Ventral. 354. Posterior.

Figures 355–362. *C. cuenca* n. sp. 355–358. Epigynum. 355. Dorsal, cleared. 356. Ventral, cleared. 357. Ventral. 358. Posterior. 359. Female. 360–362. Left male palpus. 360. Ventral. 361. Lateral. 362. Apical.

Figures 363–365. *C. monticola* (Keyserling)., male palpus. 363. Ventral. 364. Lateral. 365. Apical.

Scale lines. 0.1 mm, except Figures 338–340, 345, 350, 359, 1.0 mm.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diameter from laterals. Abdomen shield-shaped with slight shoulder humps. Total length, 5.2 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 2.7 mm; patella and tibia, 3.2 mm; metatarsus, 2.8 mm; tarsus, 1.0 mm. Second, 2.0 mm; third, 1.1 mm; fourth, 1.5 mm.

Diagnosis. The epigynum of this species differs from that of *C. bolivari* by having a narrower median scape (Fig. 348) and shorter posterior lateral plates (Fig. 349).

Chrysometa bolivari new species
Figures 351–354; Map 3

Holotype. Female from Hacienda Talahua, 3,100 m, Prov. Bolívar, Ecuador, 29 April 1939 (F. M. Brown, AMNH). The species is named after Simón Bolívar.

Description. Female. Carapace orange with symmetrical gray maculations and light median line; thorax with black on margin and white pigment spot anterior to depression; chelicerae dark orange; sternum blackish; legs ringed. Dorsum of abdomen with white pigment spots, black shoulder marks, and posterior black band having sides almost parallel. Anterior lateral eyes 1.5 diameters of anterior medians; posterior median eyes twice diameter, posterior laterals 1.3 diameters of anterior median eyes. Anterior median eyes 1.3 diameters apart, 1.3 diameters from laterals. Posterior median eyes 0.8 diameters apart, their diameter from laterals. Abdomen oval. Total length, 4.0 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 2.9 mm; patella and tibia, 3.5 mm; metatarsus, 3.1 mm; tarsus, 1.1 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.7 mm.

Note. Specimen's abdomen is in poor preservation.

Diagnosis. The epigynum of this species differs from that of *C. macintyrei* by having a wider scape (Fig. 353) on whose posterior face are a pair of widely separated openings; it also differs by having longer posterior plates (Fig. 354).

Chrysometa cuenca new species
Figures 355–362; Map 3

Holotype. Female holotype, with six female, two male paratypes from south of Cuenca, 2,500–2,800 m, Prov. Azuay, Ecuador, 15 March 1965 (L. Peña, MCZ). The specific name is a noun in apposition after the type locality.

Description. Carapace orange with black marks (Fig. 359), white spot in center of thorax; sternum dark orange, black on sides; venter orange with indistinct black rings. Dorsum of abdomen with little silver plates almost touching, posterior with black folium (Fig. 359); venter black with white longitudinal line on each side. Eyes subequal in size. Anterior median eyes slightly more than their diameter apart, 1.7 diameters from laterals. Posterior median eyes slightly more than their diameter apart, 1.7 diameters from laterals. Abdomen oval. Total length, 4.5 mm. Carapace, 2.2 mm long, 1.5 mm wide. First femur, 2.9 mm; patella and tibia, 3.5 mm; metatarsus, 3.0 mm; tarsus, 1.1 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.7 mm.

Male. Coloration like female. Total length, 3.0 mm. Carapace, 1.5 mm long, 1.1 mm wide. First femur, 2.9 mm; patella and tibia, 3.5 mm; metatarsus, 3.1 mm; tarsus, 1.0 mm. Second patella and tibia, 1.8 mm; third, 0.8 mm; fourth, 1.4 mm.

Variation. Females vary from 4.1 to 4.5 mm, males from 2.8 to 3.0 mm.

Diagnosis. The epigynum of the female differs from that of *C. macintyrei* and *C. bolivari* by having the sides of the scape parallel (Fig. 357). It differs from that of *C. eberhardi* in posterior view by having the lateral plates covering the scape (Fig. 358). The male palpus differs from that of *C. monticola* by having a smaller conductor and terminal apophysis (Figs. 360–362).

Natural History, Distribution. Found at high altitudes (2,500 m), Ecuador (Map 3).

Paratypes. ECUADOR *Prov. Pichin-*

cha: Mt. Pichincha near Quito, Aug. 1944, (W. Prescott, MCZ); Quito, ♂ (MCZ). *Cotopaxi:* 26 km N of Latacunga, 21 Feb. 1955, 2♀ (E. I. Schlinger, E. S. Ross, CAS). *Tungurahua:* Ambato, June 1943, 6♀, ♂ (H. E., D. L. Frizzell, EPC). *Azuay:* Cuenca, 3 Apr. 1942, 2♀ (H. E., D. L. Frizzell, EPC).

Chrysometa monticola (Keyserling), new combination
Figures 363–365; Map 3

Meta monticola Keyserling, 1883: 204, figs. 9, 15, ♀, ♂. Male syntype (female lost) from Montana di Nancho [mountains east of Pacasmayo, 2,600 m, Dpto. Cajamarca], Peru (PAN), examined. Roewer, 1942: 919. Bonnet, 1957: 2796.

Argyrodes monticola:—Keyserling, 1893: 328, pl. 17, fig. 243, ♀, ♂.

Description. Male. Carapace, sternum, legs orange-yellow. Dorsum of abdomen with tiny silver spots (abdomen in poor condition). Venter with two gently curved white lines; the one on the spider's left side is a slightly squeezed S, the right is its mirror image. Eyes subequal in size. Anterior median eyes their diameter apart, 1.2 diameters from laterals. Posterior median eyes their diameter apart, 1.5 from laterals. Total length, 3.4 mm. Carapace, 1.8 mm long, 1.6 mm wide. First femur, 3.5 mm; patella and tibia, 4.3 mm; metatarsus, 4.3 mm; tarsus, 1.2 mm. Second patella and tibia, 2.5 mm; third, 1.2 mm; fourth, 1.7 mm.

Note. The epigynum of the lost female pictured by Keyserling has two circular depressions divided by a septum of equal diameter. The septum might be a scape.

Diagnosis. This male differs from *C. zelotypa* by having the base of the conductor with a shelf (Fig. 363) and by having a pointed terminal apophysis lobe with a large, wide thorn at its base (Figs. 363, 364).

Chrysometa minza new species
Figures 366–372; Map 3

Holotype. Female holotype with female and male paratypes from Volcán Minza Chica, 3,500 m, Prov. Tungurahua, Ecuador, April 1939 (F. M. Brown, AMNH). The specific name is a noun in apposition after the type locality. *Note.* The type locality is Paramo Minza Chica, 1°31'S, 78°25'W (F. M. Brown, 1941).

Description. Female. Carapace orange with darker maculations and white spot anterior to thoracic depression; sternum black on orange; legs orange with dark rings. Dorsum of abdomen with large silver spots almost their diameter apart, posteriorly with a median black band with anterolateral branch (Fig. 370); sides with some silver spots; venter black with line of silver spots on each side. Secondary eyes equal to 1.8 diameters of anterior median eyes. Anterior median eyes 1.5 diameters apart, 1.8 diameters from laterals. Posterior median eyes slightly less than their diameter apart, 1.3 diameters from laterals. Abdomen oval. Total length, 4.2 mm. Carapace, 1.7 mm long, 1.5 mm wide. First femur, 2.5 mm; patella and tibia, 2.9 mm; metatarsus, 2.5 mm; tarsus, 1.1 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm; fourth, 1.6 mm.

Male. Coloration like female. Anterior lateral eyes, posterior median eyes equal to 1.2 diameters of anterior medians; posterior lateral eyes equal to 1.1 diameters of anterior median eyes. Anterior median eyes their diameter apart, slightly more than their diameter from laterals. Posterior median eyes 0.6 diameters apart, their diameter from laterals. Total length, 3.4 mm. Carapace, 1.6 mm long, 1.4 mm wide. First femur, 3.1 mm; patella and tibia, 4.0 mm; metatarsus, 3.6 mm; tarsus, 1.1 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.5 mm.

Diagnosis. The epigynum of females differs from that of *C. cuenca* by lacking a scape and from other species by having the black, median depression not bordered (Fig. 368); the male palpus differs from that of *C. cuenca* by having the basal end of the conductor enclosed by the tegulum and having the tegulum medially drawn out and pointed (Figs. 371, 372).

Chrysometa tinajillas new species
Figures 373–377; Map 3

Holotype. Female holotype with two immature paratypes from Cordillera Tinajillas, 3,100 m, south of Cuenca, Prov. Azuay, Ecuador, 18–21 March 1965 (L. Peña, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow with gray marks and white pigment spot on thorax; labium, sternum black; endites yellow; legs yellow, indistinctly ringed. Dorsum of abdomen black posteriorly, surrounded by silver spots (Fig. 377); venter black with pair of paraxial lines containing silver spots. Eyes small. Lateral eyes equal to 1.2 diameters of anterior median eyes; posterior median eyes equal to 1.3 diameters of anterior medians. Anterior median eyes 1.5 diameters apart, 2 diameters from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Total length, 4.0 mm. Carapace, 1.8 mm long, 1.5 mm wide. First femur, 2.8 mm; patella and tibia, 3.5 mm; metatarsus, 2.9 mm; tarsus, 1.1 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.8 mm.

Diagnosis. The epigynum of this species differs by having a transverse bar with a short anterior lip over a longitudinal groove (Fig. 375); it is bordered posteriorly by the posterior plates (Fig. 376).

Natural History, Distribution. Found at high elevations, Ecuador.

Paratypes. ECUADOR *Prov. Azuay:* Cerro Tinajillas, 3,100 m, 18–21 March 1965, ♀ (L. Peña, MCZ); Lago Zurucuchu, 18 km W of Cuenca, 16 Feb. 1955, ♀ (E. I. Schlinger, E. S. Ross, CAS).

Chrysometa sztolcmani new species
Figures 378–381

Holotype. Female holotype with one female paratype from Palatayoc [place not located], Peru (K. Jelski, J. Sztolcman, PAN). The species is named after the collector.

Description. Female. Carapace orange, darker on each side of head and on thoracic depression, with a median light orange line; sternum, endites black; legs orange, indistinctly ringed. Dorsum of abdomen with small silver spots almost touching, posterior two thirds with dark median band consisting of lighter and darker transverse bars, dark bars separated in middle; venter black, a light line of silver spots on each side and a silver spot on each side of spinnerets. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, 1.7 diameters from laterals. Posterior median eyes slightly more than their diameter apart, 1.7 diameters from laterals. Abdomen oval. Total length 4.8 mm. Carapace, 2.1 mm long, 1.6 mm wide. First femur, 3.0 mm; patella and tibia, 3.6 mm; metatarsus, 2.9 mm; tarsus, 1.1 mm. Second patella and tibia, 2.5 mm; third, 1.2 mm; fourth 2.0 mm.

Diagnosis. The epigynum of this species

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Figures 366–372. *Chrysometa minza* n. sp. 366–369. Epigynum. 366. Dorsal, cleared. 367. Ventral, cleared. 368. Ventral. 369. Posterior. 370. Female. 371–372. Left male palpus. 371. Ventral. 372. Lateral.

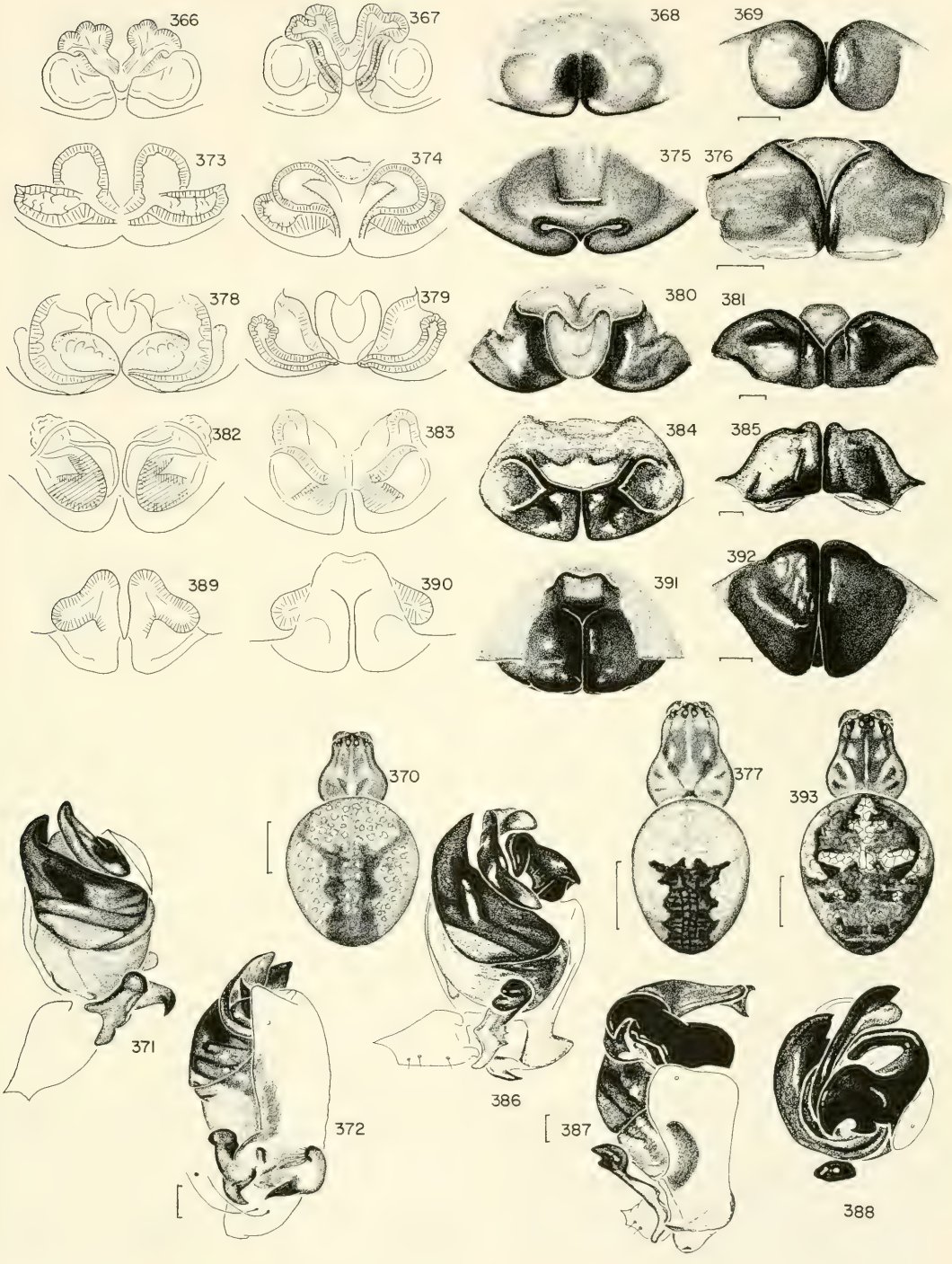
Figures 373–377. *C. tinajillas* n. sp. 373–376. Epigynum. 373. Dorsal, cleared. 374. Ventral, cleared. 375. Ventral. 376. Posterior. 377. Female.

Figures 378–381. *C. sztolcmani* n. sp., epigynum. 378. Dorsal, cleared. 379. Ventral, cleared. 380. Ventral. 381. Posterior.

Figures 382–388. *C. chica* n. sp. 382–385. Epigynum. 382. Dorsal, cleared. 383. Ventral, cleared. 384. Ventral. 385. Posterior. 386–388. Male palpus. 386. Ventral. 387. Lateral. 388. Apical.

Figures 389–393. *C. browni* n. sp. 389–392. Epigynum. 389. Dorsal, cleared. 390. Ventral, cleared. 391. Ventral. 392. Posterior. 393. Female.

Scale lines. 0.1 mm, except Figures 370, 377, 393, 1.0 mm.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differs from all others by having a median light-colored, heart-shaped knob (Fig. 380).

Chrysometa chica new species
Figures 382–288; Map 3

Holotype. Female holotype with four female and one male paratypes from Volcán Minza Chica, 3,500 m, Prov. Tungurahua, Ecuador, April 1939 (F. M. Brown, AMNH). The specific name is an arbitrary combination of letters. *Note.* The locality is paramo Minza Chica, 1°31'S, 78°25'W (F. M. Brown, 1941).

Description. Female. Carapace, legs orange-yellow; sternum dusky orange-yellow. Dorsum of abdomen with black spots, densest on sides, and median gray band darkest posteriorly; sides gray; venter with black band and white longitudinal line on each side. Secondary eyes equal to 1.5 diameters of anterior median eyes. Anterior median eyes 1.7 diameters apart, 2 diameters from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Abdomen oval. Total length, 5.6 mm. Carapace, 2.1 mm long, 1.6 mm wide. First femur, 2.8 mm; patella and tibia, 3.3 mm; metatarsus, 2.8 mm; tarsus, 1.2 mm. Second patella and tibia, 2.3 mm; third, 1.2 mm; fourth, 1.9 mm.

Male. Coloration and eye structure like female. Anterior median eyes their diameter apart, 1.5 diameters from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Total length, 4.0 mm. Carapace, 2.1 mm long, 1.8 mm wide. First femur, 3.2 mm; patella and tibia, 4.2 mm; metatarsus, 3.7 mm; tarsus, 1.2 mm. Second patella and tibia, 2.5 mm; third, 1.1 mm; fourth, 1.8 mm.

Diagnosis. The epigynum of the female differs from all others by having a wide, median anterior lobe and lateral depressions (Fig. 384). The male differs from *C. minza* and *C. bolivari* by having a relatively small, narrow conductor that is lobed distally (Figs. 386–388).

Chrysometa browni new species
Figures 389–393; Map 3

Holotype. Female holotype with one female paratype from Volcán Minza Chica, 3,500 m, Prov. Tungurahua, Ecuador, April 1939 (F. M. Brown, AMNH). The species is named after the collector. *Note.* The type locality is paramo Minza Chica, 1°31'S, 78°25'W (F. M. Brown, 1941).

Description. Female. Carapace with black marks on orange, head black to thoracic depression, orange around lateral eyes and a fine median orange line; sides of thorax with two black marks and black margin (Fig. 393). Sternum black; legs orange with narrow black rings. Dorsum of abdomen with silver spots, posteriorly with gray marks and black transverse bars forming a longitudinal band; sides gray; venter black with line of silver spots on each side. Secondary eyes equal to 1.5 diameters of anterior median eyes. Anterior median eyes 1.5 diameters apart, same distance from laterals. Posterior median eyes 0.8 diameters apart, 1.2 diameters from laterals. Abdomen oval, widest anteriorly. Total length, 4.8 mm. Carapace, 2.0 mm long, 1.7 mm wide. First femur, 3.3 mm; patella and tibia, 4.2 mm; metatarsus, 3.4 mm; tarsus, 1.3 mm. Second patella and tibia, 2.7 mm; third, 1.3 mm; fourth, 2.1 mm.

Diagnosis. The epigynum of this species differs from all others by having an anterior median lobe bearing a light rectangular patch (Fig. 391).

Chrysometa luisi new species
Figures 394–401; Map 3

Holotype. Female holotype and male paratype from Cerro Tinajillas, 3,100 m, Azuay Prov., Ecuador, 18–21 March 1965 (L. Peña, MCZ). This species is named after the collector.

Description. Female. Carapace similar to *C. troya*, but more contrasting, with median light line (Fig. 398); sternum black; legs with indistinct narrow rings. Dorsum of abdomen with scattered white spots and darker pattern than in *C. troya*. Eyes subequal in size. Anterior median

eyes their diameter apart, 1.5 diameters from laterals. Posterior median eyes slightly less than their diameter apart, 1.7 diameters from laterals. Abdomen oval. Total length, 5.0 mm. Carapace, 1.8 mm long, 1.6 mm wide. First femur, 3.2 mm; patella and tibia, 3.8 mm; metatarsus, 3.4 mm; tarsus, 1.3 mm. Second patella and tibia, 2.3 mm; third, 1.1 mm; fourth, 1.9 mm.

Male. Darker than female. Carapace blackish orange on sides with some areas darker brown; endites, sternum black; coxae gray; legs orange-yellow with indistinct gray rings. Abdomen with silver spots and black behind as in female, also black anteriorly on sides and on venter. Eyes subequal in size. Anterior median eyes their diameter apart, 1.5 diameters from laterals. Posterior median eyes their diameter apart, 1.7 diameters from laterals. Total length, 4.5 mm. Carapace, 2.1 mm long, 1.8 mm wide. First femur, 4.7 mm; patella and tibia, 5.8 mm; metatarsus, 6.2 mm; tarsus, 1.7 mm. Second patella and tibia, 3.2 mm; third, 1.4 mm; fourth, 2.3 mm.

Diagnosis. The epigynum of females is distinguished from others by the wide median lobe overhanging a sclerotized depression (Fig. 396); the male palpus differs from others by the large conductor and biforked embolus-terminal apophysis tip (Figs. 399–401).

Chrysometa allija new species
Figures 402–408; Map 3

Holotype. Female holotype and one female paratype from Cerro Tinajillas, 3,100 m, Prov. Azuay, Ecuador, 18–21 March 1965 (L. Peña, MCZ). The name is an arbitrary combination of letters.

Description. Female. Carapace orange, gray on each side of head and middle of thorax. Sternum brown; legs orange with indistinct black rings. Dorsum of abdomen with silver spots less than their diameter apart. Sides with black patch anteriorly; posteriorly with wide, dark median longitudinal band as in *C. chiriqui.* Venter black with longitudinal white band on each side. Eyes subequal in size. Anterior median eyes their diameter apart, 1.4 diameters from laterals. Posterior median eyes slightly more than their diameter apart, 1.7 from laterals. Abdomen oval. Total length, 4.0 mm. Carapace, 2.1 mm long, 1.5 mm wide. First femur, 3.0 mm; patella and tibia, 3.7 mm; metatarsus, 2.9 mm; tarsus, 1.0 mm. Second patella and tibia, 2.4 mm; third, 1.3 mm; fourth 1.9 mm.

Male. Coloration like female. Eyes subequal in size. Anterior median eyes their diameter apart, 1.4 diameters from laterals. Posterior median eyes 1.3 diameters apart, two diameters from laterals. Total length, 4.5 mm. Carapace, 2.7 mm long, 2.1 mm wide. First femur, 4.6 mm; patella and tibia, 5.6 mm; metatarsus, 5.4 mm; tarsus, 1.5 mm. Second patella and tibia, 3.5 mm; third, 1.5 mm; fourth, 2.5 mm.

Variation. Females vary from 4.0 to 6.7 mm total length.

Diagnosis. The epigynum of this species has two facing lobes with an opening at the lateral end of their anterior borders (Fig. 404). The male palpus differs from others by the twisted distal end of the conductor and the shape of the embolus and terminal apophysis (Figs. 406–408).

Natural History. Found at 3,000 m altitude, Ecuador (Map 3).

Paratypes. ECUADOR. *Prov. Bolívar:* Hda. Talahua, 3,100 m, 29 April 1939, ♀ (F. M. Brown, AMNH). *Chimborazo:* Urbina, 3,650 m, Cerro Chimborazo, 18 April 1939, 9♀, 2♂ (F. M. Brown, AMNH). *Azuay:* 52 km S of Cuenca, 3,200 m, 21 March 1965, 5♀, 12 imm. (L. Peña, MCZ).

Chrysometa ura new species
Figures 409–412; Map 3

Holotype. Female from Volcán Minza Chica, 3,500 m, Prov. Tungurahua, Ecuador (F. M. Brown, AMNH). The species is an arbitrary combination of letters. *Note.* The locality is paramo Minza Chica, 1°31′S, 78°26′W (F. M. Brown, 1941).

Description. Female. Carapace orange with indistinct dark gray marks, white pigment spot in front of thoracic depression; sternum orange with black pigment; legs orange with dark narrow rings. Dorsum of abdomen marked as in other species, with scattered silver spots, gray on shoulders, posteriorly with transverse black marks forming longitudinal band; sides gray; venter with longitudinal line of silver spots on each side. Anterior lateral eyes equal to 1.5 diameters of anterior medians; posterior eyes equal to 1.7 diameters of anterior median eyes. Anterior median eyes 1.5 diameters apart, same distance from laterals. Posterior median eyes 0.7 diameters apart, slightly less than their diameter from laterals. Abdomen subspherical, widest anteriorly. Total length, 3.7 mm. Carapace, 1.6 mm long, 1.3 mm wide. First femur, 2.3 mm; patella and tibia, 2.8 mm; metatarsus, 2.2 mm; tarsus, 0.9 mm. Second patella and tibia, 1.7 mm; third, 0.9 mm; fourth, 1.4 mm.

Diagnosis. Unlike the epigynum of *C. allija*, the facing lobes are separated from each other and their anterior margin surrounds a depression anteriorly on each side (Fig. 411).

Chrysometa troya new species
Figures 413–420; Map 3

Holotype. Female holotype and twelve females, 10 male paratypes from Troya, 2,900–2,950 m, Prov. Carchi, Ecuador, 10–13 June 1965 (L. Peña, MCZ).

The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange-brown with darker markings, sternum black; coxae orange; legs orange-brown with indistinct darker marks. Dorsum of abdomen with silver spots and black marks (Fig. 417); venter with pair of lines of silver spots. Eyes subequal in size. Anterior median eyes 1.2 diameters apart, 2 diameters from laterals. Posterior median eyes 1.2 diameters apart, 1.8 diameters from laterals. Abdomen oval. Total length, 5.2 mm. Carapace, 2.5 mm long, 1.9 mm wide. First femur, 3.5 mm; patella and tibia, 4.3 mm; metatarsus, 3.1 mm; tarsus, 1.2 mm. Second patella and tibia, 2.7 mm; third, 1.3 mm; fourth, 2.0 mm.

Male. Coloration like female. Eyes subequal in size. Anterior median eyes slightly more than their diameter apart, 2 diameters from laterals. Posterior median eyes slightly more than their diameter apart, 2 diameters from laterals. Total length, 4.5 mm. Carapace, 2.5 mm long, 1.8 mm wide. First femur, 4.2 mm; patella and tibia, 5.2 mm; metatarsus, 5.1 mm; tarsus, 1.5 mm. Second patella and tibia, 3.0 mm; third, 1.3 mm; fourth, 2.2 mm.

Variation. Females vary in total length from 3.5 to 5.0 mm, males from 4.5 to 5.2 mm.

Diagnosis. The epigynum of females differs from that of *C. purace* by having the lateral, anterior margins of the depression continue medially into a septum (Fig.

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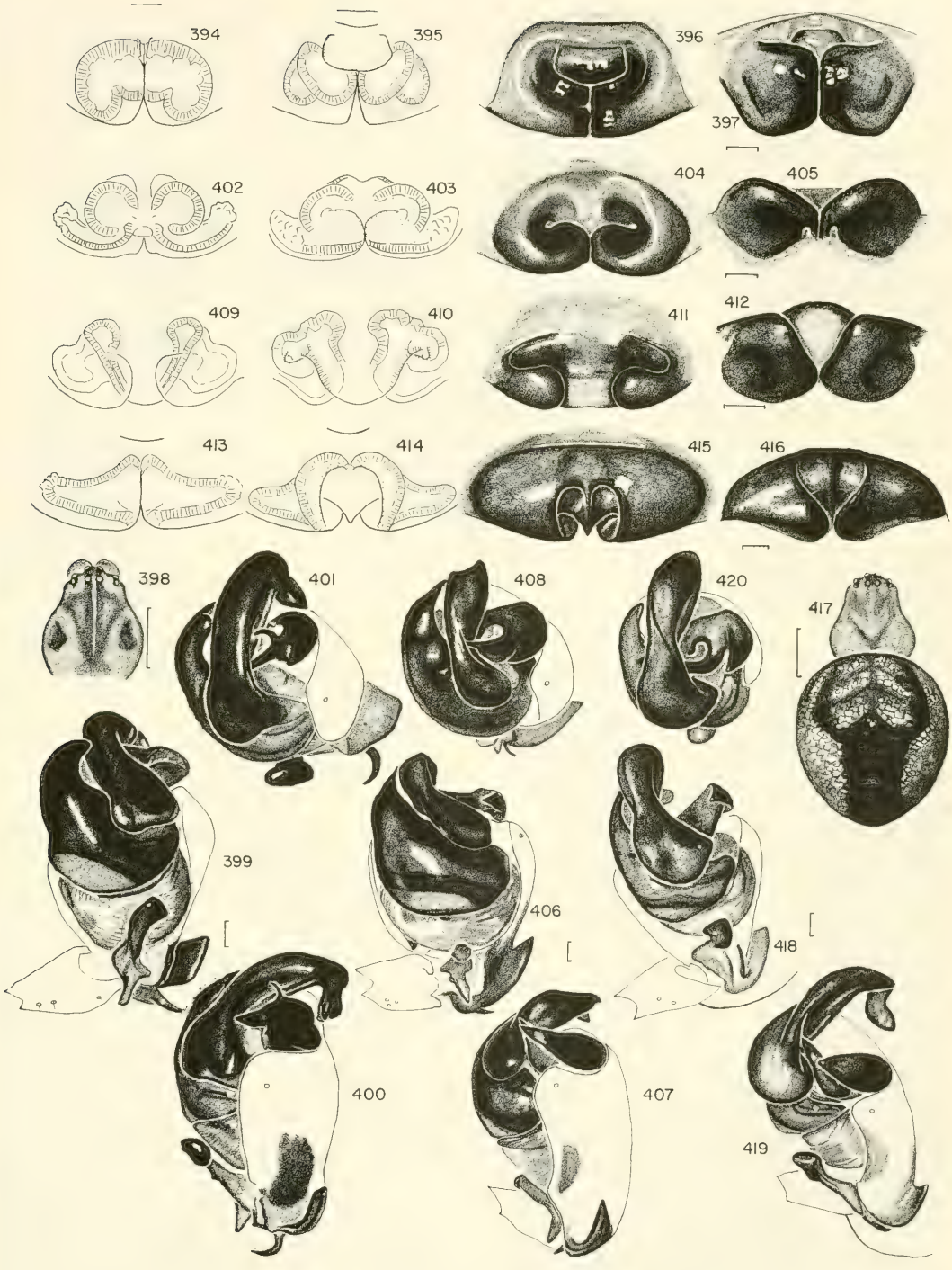
Figures 394–401. *Chrysometa luisi* n. sp. 394–397. Epigynum. 394. Dorsal, cleared. 395. Ventral, cleared. 396. Ventral. 397. Posterior. 398. Female carapace. 399–401. Left male palpus. 399. Ventral. 400. Lateral. 401. Apical.

Figures 402–408. *C. allija* n. sp. 402–405. Epigynum. 402. Dorsal, cleared. 403. Ventral, cleared. 404. Ventral. 405. Posterior. 406–408. Male palpus. 406. Ventral. 407. Lateral. 408. Apical.

Figures 409–412. *C. ura* n. sp., epigynum. 409. Subdorsal, cleared. 410. Subventral, cleared. 411. Ventral. 412. Posterior.

Figures 413–420. *C. troya* n. sp. 413–416. Epigynum. 413. Dorsal, cleared. 414. Ventral, cleared. 415. Ventral. 416. Posterior. 417. Female. 418–420. Male palpus. 418. Ventral. 419. Lateral. 420. Apical.

Scale lines. 0.1 mm, except Figures 398, 417, 1.0 mm.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415). The male palpus differs from that of *C. purace* by having the conductor with an s-shaped tip and by the shape of embolus and terminal apophysis (Figs. 418–420).

Natural History, Distribution. Found 1,800 to 3,100 m, Ecuador (Map 3).

Paratypes. ECUADOR *Prov. Carchi:* Troya, 2,900 m, 10–13 June 1965, 3♀, ♂ (L. Peña, MCZ); Volcán Chiles, 2,000–3,100 m, 26, 27 June 1965, ♀ (L. Peña, MCZ); Cerro Pelado, S of Tulcán, 3,200 m, 25 June 1965, 2♀, 16 imm. (L. Peña, MCZ); Tulcán, El Carmelo, 3,350 m, 11 Sept. 1977, 9♀, 8♂ (L. Peña, AMNH). *Zamora-Chinchipe:* Zamora, 1,800–2,200 m, 28 Oct. 1977, ♀ (L. Peña, AMNH).

Chrysometa purace new species
Figures 421–428; Map 3

Holotype. Female holotype and one male paratype from Paramo Puracé, 11,000 ft. [3,500 m], Dpto. Huila, Colombia, March 1976 (W. Eberhard, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, legs orange-yellow and gray; chelicerae dark orange; sternum black. Dorsum of abdomen with two longitudinal black bands (Fig. 425); venter black with curved longitudinal line of silver spots on each side; white spot on each side anterior of spinnerets. Anterior lateral eyes 1.2 diameters of anterior median eyes. Posterior median eyes 1.2 diameters of anterior medians, posterior laterals 1.1 diameters. Anterior median eyes slightly more than their diameter apart, same distance from laterals. Posterior median eyes slightly less than their diameter apart, 1.5 diameters from laterals. Abdomen narrow oval (Fig. 425). Total length, 4.8 mm. Carapace, 1.9 mm long, 1.3 mm wide. First femur, 2.5 mm; patella and tibia, 3.2 mm; metatarsus, 2.7 mm; tarsus, 1.0 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.8 mm.

Male. Coloration like female. Carapace with deep thoracic depression. Eyes sizes like female. Anterior median eyes their diameter apart, same distance from laterals. Posterior median eyes slightly less than their diameter apart, 1.5 diameters from laterals. Abdomen narrow oval. Total length, 4.5 mm. Carapace, 2.1 mm long, 1.7 mm wide. First femur, 3.4 mm; patella and tibia, 4.5 mm; metatarsus, 4.2 mm; tarsus, 1.2 mm. Second patella and tibia, 2.7 mm; third, 1.2 mm; fourth, 2.0 mm.

Diagnosis. The epigynum differs from that of *C. troya* by having the lip surrounding the depression entire (Fig. 423). The male palpus differs by the knobbed tip of the conductor and the shape of the embolus and terminal apophysis (Figs. 426–428).

Chrysometa merida new species
Figures 429–431; Map 3

Holotype. Male from La Culata, 2,850 m, Est. Mérida, Venezuela, Feb. 1968 (J. Rivero, MCZ). The specific name is a noun in apposition after the type locality.

Description. Male. Carapace orange with pair of paraxial median longitudinal black lines separated by a light line; labium black; sternum black, orange in center; legs orange-gray. Dorsum of abdomen without silver spots, pair of indistinct gray anterior brackets, posteriorly a longitudinal dark band consisting of black transverse bars; venter gray with light longitudinal band on each side. Carapace with deep longitudinal thoracic groove. Eyes subequal in size. Anterior median eyes their diameter apart, slightly less than two diameters from laterals. Posterior median eyes their diameter apart, 1.8 diameters from laterals. Abdomen oval, elongate. Total length, 5.8 mm. Carapace, 2.7 mm long, 2.2 mm wide. First femur, 4.8 mm; patella and tibia, 5.7 mm; metatarsus, 5.9 mm; tarsus, 1.5 mm. Second patella and tibia, 3.7 mm; third, 1.7 mm; fourth, 2.7 mm.

Diagnosis. This male palpus differs from others of this species group by having a relatively small conductor like *C. chica* and by the shape of the embolus and terminal apophysis (Figs. 429–431).

Figures 421–428. *Chrysometa purace* n. sp. 421–424. Epigynum. 421. Dorsal, cleared. 422. Ventral, cleared. 423. Ventral. 424. Posterior. 425. Female. 426–428. Left male palpus. 426. Ventral. 427. Lateral. 428. Apical.

Figures 429–431. *C. merida* n. sp., male palpus. 429. Ventral. 430. Lateral. 431. Apical.

Figures 432–434. *C. huanuco* n. sp., male palpus. 432. Ventral. 433. Lateral. 434. Apical.

Scale lines. 0.1 mm, except Figure 425, 1.0 mm.

Chrysometa huanuco new species
Figures 432–434; Map 3

Holotype. Male from Huánuco, Dpto. Huánuco, Peru, 16 Sept. 1954 (E. I. Schlinger, E. S. Ross, CAS). The specific name is a noun in apposition after the type locality.

Description. Male. Carapace dusky orange with median light orange line; sternum black; legs orange with indistinct rings. Dorsum of abdomen with silver spots, posterior dark longitudinal band, and dark patches on shoulders. Venter

black with a silver longitudinal line on each side. Anterior lateral eyes equal to 1.3 diameters of anterior medians; posterior medians equal to 1.5 diameters; posterior laterals equal to diameter of anterior median eyes. Anterior median eyes their diameter apart, 1.5 diameters from laterals. Posterior median eyes their diameter apart, 1.8 diameters from laterals. Abdomen oval. Total length, 4.0 mm. Carapace, 1.9 mm long, 1.6 mm wide. First femur, 3.9 mm; patella and tibia, 4.8 mm; metatarsus, 4.7 mm; tarsus, 1.3 mm. Second patella and tibia, 2.7 mm; third, 1.3 mm; fourth, 2.0 mm.

Diagnosis. The male palpus differs from those of *C. chica* and *C. merida*, which also have a small conductor, by the shape of the embolus and terminal apophysis (Figs. 432–434).

Paratypes. PERU *Dpto. Huánuco:* Sariapampa, 3,600 m, 4♂ (F. Woytkowski, AMNH).

Chrysometa minuta (Keyserling), new combination
Figures 435–440; Map 3

Meta minuta Keyserling, 1883: 206, pl. 15, fig. 10, ♀. Female from "Province Amazonas," Brazil (HEO), examined. Roewer, 1942: 919. Bonnet, 1957: 2795.

Argyroepeira minuta Keyserling, 1893: 321, pl. 16, fig. 236, ♀.

Description. Female. Carapace, sternum, legs light orange. Dorsum of abdomen bleached orange-white [according to Keyserling, with fine white spots]. Anterior lateral eyes, posterior median eyes equal to 0.8 diameters of anterior medians; posterior lateral eyes equal to 0.6 diameters of anterior median eyes. Anterior median eyes 0.3 diameters apart, same distance from laterals. Posterior medians slightly less than their diameter apart, slightly more than their diameter from laterals. Abdomen subspherical. Total length, 3.5 mm. Carapace, 1.4 mm long, 1.1 mm wide. First femur, 1.9 mm; patella and tibia 1.5 mm. Second patella and tibia, 1.7 mm; third, 0.8 mm; fourth, 1.4 mm.

Variation. Recently collected specimens have scattered tiny white spots covering the abdomen and posteriorly on the abdomen paired, transverse, dusky marks (Fig. 440).

Diagnosis. The epigynum of this species differs from that of *C. aureola* by having the median septum posteriorly surrounded by lobes (Figs. 437, 438).

Natural History, Distribution. Found in low elevation forest of the Amazon area (Map 3).

Records. BRAZIL *Est. Amazonas:* Manaus, Aug. 1971, ♀ (M. E. Galiano, MG). *Mato Grosso:* Synoptic coll., 5♀ (M. Alvarenga, AMNH); 260 km N of Xavantina [12°49′S, 51°46′W], 400 m, gallery and dry forest, Feb.–April 1969, 2♀ (Xavantina-Cachimbo Exped., MCZ, MZSP).

Chrysometa aureola (Keyserling), new combination
Figures 441–446; Map 3

Zilla aureola Keyserling, 1884: 652, pl. 21, fig. 4, ♀. Two female paratypes in poor physical condition from le Para [Belém], Brazil in the MNHN, Paris, examined. Published locality: Pevas [Pebas, Peru]. Keyserling, 1893: 300, pl. 15, fig. 221, ♀.

Araneus aureola:—Petrunkevitch, 1911: 281.

Zygiella aureola:—Roewer, 1942: 886. Bonnet, 1959: 5001.

Note. The types had been marked *Meta aureola*, possibly by Simon.

Description. Female. Carapace, legs yellowish white; sternum yellow-brown. Dorsum and sides of abdomen with scattered white pigment spots evenly distributed. The spots were described by Keyserling (1884) as yellow. Anterior lateral eyes 0.7 diameters of anterior median eyes; posterior median and lateral eyes 0.8 diameters of anterior medians. Anterior median eyes slightly less than their diameter apart, same distance from laterals. Posterior median eyes slightly less than their diameter apart, slightly more than one diameter from laterals. Abdomen subspherical. Total length, 3.2 mm. Carapace, 1.3 mm long, 0.9 mm wide. First femur, 1.7 mm; patella and tibia, 2.2 mm; metatarsus, 1.8 mm; tarsus, 0.7 mm. Second pa-

tella and tibia, 1.5 mm; third, 0.8 mm; fourth, 1.2 mm.

Male from Trinidad. Carapace orange, coloration otherwise like female. Lateral eyes equal to 0.6 diameters of anterior median eyes; posterior median eyes 0.7 diameters of anterior median eyes. Anterior median eyes 0.7 diameters apart, same distance from laterals. Posterior median eyes slightly less than their diameter apart, 1.2 diameters from laterals. Abdomen oval. Total length, 2.2 mm. Carapace, 1.2 mm long, 0.9 mm wide. First femur, 1.7 mm; patella and tibia, 2.0 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm. Second patella and tibia, 1.5 mm; third, 0.7 mm; fourth, 1.0 mm.

Variation. Total length of females from 2.5 to 3.2 mm.

Diagnosis. The epigynum differs from that of *C. minuta* by having the septum touch the posterior margin of the epigynum in ventral view (Fig. 443) and from *C. xavantina* by the round lateral plates in posterior view. The male palpus differs from that of *C. xavantina* by the shape of the tips of conductor, embolus and terminal apophysis (Figs. 445, 446).

Records. TRINIDAD Piarco, 27 Nov. 1954, 2♀, ♂, 3–6 Jan. 1955, ♀ (A. M. Nadler, AMNH).

Chrysometa xavantina new species
Figures 447-453; Map 3

Holotype. Carapace, palpi and leg fragments of male holotype and abdomen of female paratype from 260 km N of Xavantina, 12°49'S, 51°46'W, 400 m el., Est. Mato Grosso, Brazil, Feb.–April 1969 (Xavantina–Cachimbo Exped., MZSP, ex MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Abdomen oval, covered by small white pigment spots.

Male. Carapace, sternum orange-brown, legs yellowish. Carapace with shallow thoracic depression. Secondary eyes 0.8 diameters of anterior medians. Anterior median eyes their diameter apart, 0.6 from laterals. Posterior median eyes slightly less than their diameter apart, their diameter from laterals. Clypeus height equal to 1.5 diameters of anterior median eyes. Carapace, 1.3 mm long, 1.0 mm wide. First femur, 2.2 mm. Third patella and tibia, 0.8 mm.

Diagnosis. The epigynum differs from that of *C. aureola* in having the posterior plates wider than long (Fig. 450) and the internal ducts wider (Figs. 447, 448). The male palpus differs from that of *C. aureola* by the shape of the tips of conductor and terminal apophysis and also by the paracymbium, which has a 90° angle in ventral view (Figs. 452, 453).

Chrysometa valle new species
Figures 454–458; Map 3

Holotype. Female from near Saladito, 1,600 m, Dpto. Valle, Colombia, Sept. 1975 (W. Eberhard, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange-yellow, head to thoracic depression brown. Sternum orange-yellow; legs ringed brown on orange-yellow. Dorsum of abdomen with black pattern and only scattered tiny silver spots (Fig. 458); venter black with narrow, pigmentless longitudinal line on each side containing some silver spots, and a pigmentless patch on each side anterior to pedicel. Eyes subequal in size. Anterior median eyes 0.6 diameters apart, 0.5 diameters from laterals. Posterior median eyes 0.6 diameters apart, their diameter from laterals. Abdomen oval, pointed behind. Total length, 4.0 mm. Carapace, 2.1 mm long, 1.5 mm wide. First femur, 2.9 mm; patella and tibia, 3.6 mm; metatarsus, 2.5 mm; tarsus, 1.1 mm. Second patella and tibia, 2.4 mm; third, 1.3 mm; fourth, 1.9 mm.

Diagnosis. The epigynum of this species can be separated from that of others by the circular septum and paired dark marks anterior and to the sides of the septum (Fig. 456).

Chrysometa antonio new species
Figures 459–462; Map 3

Holotype. Female from Río Donachui, 2,800 m, Sierra Nevada de Santa Marta, Colombia, 2 Jan. 1974

(J. A. Kochalka, MCZ). The specific name is a noun in apposition after one of the collecting localities.

Description. Female. Carapace orange-yellow with two gray paraxial bands; sternum, legs orange-yellow. Dorsum of abdomen with dark mark in middle, paired dark marks at posterior end; no white spots. Venter with black band, anterior half narrower than posterior. Secondary eyes equal to 1.2 diameters of anterior medians. Anterior median eyes their diameter apart, 1.2 diameters from laterals. Posterior median eyes 0.7 diameters apart, their diameter from laterals. Abdomen elongate oval. Total length, 5.0 mm. Carapace, 2.1 mm long, 1.6 mm wide. First femur, 3.5 mm; patella and tibia, 4.5 mm; metatarsus, 3.6 mm; tarsus, 1.3 mm. Second patella and tibia, 2.9 mm; third, 1.4 mm; fourth, 2.1 mm.

Variation. Two of the specimens have epigynum less sclerotized. In one specimen the anterior edge of the middle piece of the epigynum was not clearly set off.

Diagnosis. The epigynum of this species differs from that of *C. valle* by the shape of the median septum, constricted in the middle, and by the placement of the paired dark patches (Fig. 461).

Natural History, Distribution. Found 1,500 to 2,800 m elevation in northern Colombia (Map 3).

Paratypes. COLOMBIA *Dpto. Magdalena,* Sierra Nevada de Santa Marta: San Pedro, 1,500 m, 29 March 1975, ♀, 3 imm. (J. A. Kochalka, MCZ); Casa Antonio, Loma Cebolleta, 2,700 m, 8 May 1975, ♀, imm. (J. A. Kochalka).

Chrysometa nuevagranada new species
Figures 463–467; Map 3

Holotype. Female from Serra Nueva Granada, 1,570 m, Sierra Nevada de Santa Marta, Dpto. Magdalena, Colombia, 28 June 1975 (J. Kochalka, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace light orange; sternum orange; legs orange, distal ends of first tibiae black. Dorsum of abdomen without white spots, with indistinct gray shoulder patches, posteriorly with median longitudinal band consisting of transverse bars; venter with constricted black mark (Fig. 467). Eyes subequal in size. Anterior median eyes their diameter apart, slightly more than their diameter from laterals. Posterior median eyes their diameter apart, 1.3 diameters from laterals. Abdomen oval. Total length, 4.5 mm. Carapace, 2.0 mm long, 1.4 mm wide. First femur, 2.8 mm; patella and tibia, 3.5 mm; metatarsus, 2.8 mm; tarsus, 1.1 mm. Second patella and tibia, 2.3 mm; third, 1.1 mm; fourth, 1.8 mm.

Diagnosis. The epigynum of this species differs from that of *C. valle* and *C. antonio* by the subtriangular septum (Fig. 465).

Chrysometa sumare new species
Figures 468–471; Map 3

Holotype. Female from Teresópolis, 900–1,000 m, Est. Rio de Janeiro, Brazil, March 1946 (H. Sick, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange-yellow with narrow, darker median streak;

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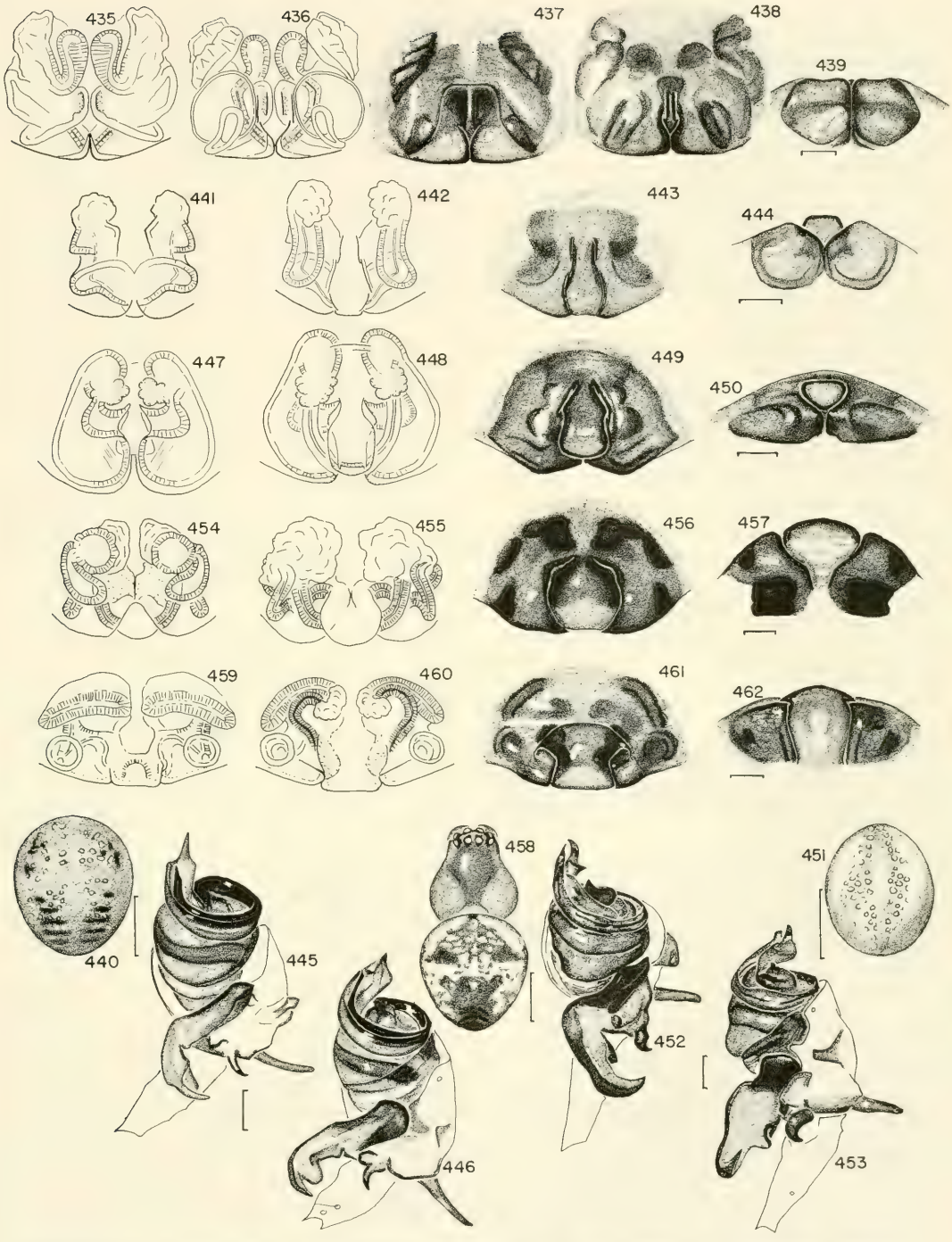
Figures 435–440. *Chrysometa minuta* (Keyserling). 435–439. Epigynum. 435. Dorsal, cleared. 436. Ventral, cleared. 437, 438. Ventral. 439. Posterior. 440. Female abdomen, dorsal. 435–437, 439. ("Amazonas"). 438, 440. (Mato Grosso).

Figures 441–446. *C. aureola* (Keyserling). 441–444. Epigynum. 441. Dorsal, cleared. 442. Ventral, cleared. 443. Ventral. 444. Posterior. 445, 446. Left male palpus. 445. Ventral. 446. Lateral.

Figures 447–453. *C. xavantina* n. sp. 447–450. Epigynum. 447. Dorsal, cleared. 448. Ventral, cleared. 449. Ventral. 450. Posterior. 451. Female abdomen, dorsal. 452, 453. Male palpus. 452. Ventral. 453. Lateral.

Figures 454–458. *C. valle* n. sp. 454–457. Epigynum. 454. Dorsal, cleared. 455. Ventral, cleared. 456. Ventral, 457. Posterior. 458. Female.



Figures 459–462. *C. antonio* n. sp., epigynum. 459. Dorsal, cleared. 460. Ventral, cleared. 461. Ventral. 462. Posterior. Scale lines. 0.1 mm, except Figures 440, 451, 458, 1.0 mm.

sternum orange; legs orange with dusky rings. Dorsum of abdomen with scattered white spots, posterior with transverse black bars forming wide longitudinal band, black patches on shoulders; sides with scattered white spots, black patch anteriorly; venter with rectangular black area anteriorly, no white lines. Eyes subequal in size. Anterior median eyes 0.8 diameters apart, 0.6 diameters from laterals. Posterior median eyes 0.6 diameters apart, their diameter from laterals. Abdomen oval. Total length, 4.5 mm. Carapace, 2.0 mm long, 1.6 mm wide. First femur, 2.7 mm; patella and tibia, 3.2 mm; metatarsus, 2.5 mm; tarsus, 0.9 mm. Second patella and tibia, 2.3 mm; third, 1.2 mm; fourth, 1.8 mm.

Variation. Total length 4.1 to 4.5 mm.

Diagnosis. The epigynum of *C. sumare* differs from others by the long, narrow transverse bar and septum (Fig. 470) and from *C. chulumani* and *C. sevillano* by longer ducts (Figs. 468, 469).

Natural History, Distribution. Found at low elevations, southeastern Brazil (Map 3).

Paratypes. BRAZIL *Est. Rio de Janeiro:* Sumaré, Rio de Janeiro, Feb. 1946, ♀ (H. Sick, AMNH). *São Paulo:* Mata do Governor, Inst. Botânica, 4 March 1959, ♀ (F. Lane, AMNH).

Chrysometa niebla new species
Figures 472–476, Map 3

Holotype. Female from Saladito, above Cali, 1,800 m, fog forest, Dpto. Valle, Colombia, 3 Jan. 1977 (H. Levi, MCZ). The specific name is a noun in apposition after niebla, Spanish for fog.

Description. Female. Carapace orange, head darker; sternum orange; legs orange, indistinctly ringed. Dorsum of abdomen with black transverse marks and few small scattered silver spots (Fig. 476); sides gray; venter black and orange-gray. Eyes subequal in size. Anterior median eyes 0.5 diameters apart, same distance from laterals. Posterior median eyes 0.5 diameters apart, 0.8 diameters from laterals. Abdomen oval. Total length, 4.2 mm. Carapace, 2.0 mm long, 1.5 mm wide. First femur, 2.7 mm; patella and tibia, 3.4 mm; metatarsus, 2.5 mm; tarsus, 1.1 mm. Second patella and tibia, 2.3 mm; third, 1.2 mm; fourth, 1.8 mm.

Diagnosis. The rectangular septum and bar of the epigynum and the surrounding pairs of dark patches distinguish this species from *C. valle* and *C. antonio* (Fig. 474).

Chrysometa buga new species
Figures 477–481; Map 3

Holotype. Female from Lago Colima between Buga and Lobguerrero, Dpto. Valle, Colombia, Sept. 1973 (W. Eberhard, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, sternum orange-yellow; legs with black rings on distal ends of tibiae. Dorsum of abdomen with tiny silver spots (Fig. 481); some gray on midline of venter. Anterior lateral eyes, posterior median eyes equal to 1.3

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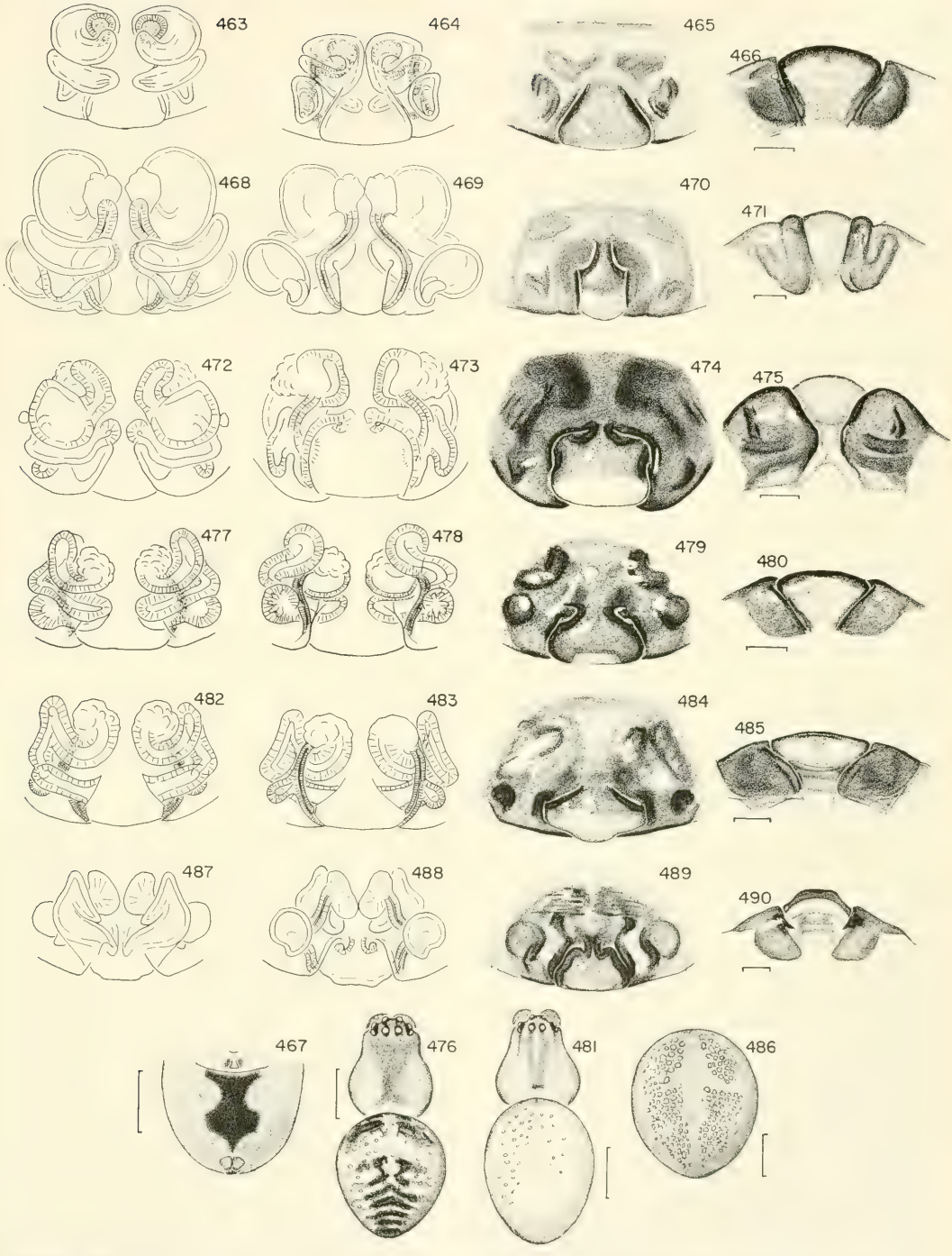
Figures 463–467. *Chrysometa nuevagranada* n. sp. 463–466. Epigynum. 463. Dorsal, cleared. 464. Ventral, cleared. 465. Ventral. 466. Posterior. 467. Female abdomen, ventral.

Figures 468–471. *C. sumare* n. sp., epigynum. 468. Dorsal, cleared. 469. Ventral, cleared. 470. Ventral. 471. Posterior.

Figures 472–476. *C. niebla* n. sp. 472–475. Epigynum. 472. Dorsal, cleared. 473. Ventral, cleared. 474. Ventral. 475. Posterior. 476. Female.

Figures 477–481. *C. buga* n. sp. 477–480. Epigynum. 477. Dorsal, cleared. 478. Ventral, cleared. 479. Ventral. 480. Posterior. 481. Female.

Figures 482–486. *C. rubromaculata* (Keyserling). 482–485. Epigynum. 482. Dorsal, cleared. 483. Ventral, cleared. 484. Ventral. 485. Posterior. 486. Female abdomen, dorsal.



Figures 487–490. *C. rincon* n. sp., epigynum. 487. Dorsal, cleared. 488. Ventral, cleared. 489. Ventral. 490. Posterior. *Scale lines.* 0.1 mm, except Figures 467, 476, 481, 486, 1.0 mm.

diameters of anterior median eyes; posterior lateral eyes equal to diameter of anterior median eyes. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes 0.8 diameters apart, 1.2 diameters from laterals. Abdomen oval. Total length, 4.5 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 3.0 mm; patella and tibia, 3.6 mm; metatarsus, 3.2 mm; tarsus, 1.2 mm. Second patella and tibia, 2.3 mm; third, 1.2 mm; fourth, 1.8 mm.

Variation. Females vary in total length from 4.0 to 4.5 mm.

Diagnosis. The wide septum, oval transverse bar and the position of the paired dark patches of the epigynum separate this species from *C. niebla* and *C. valle* (Fig. 479).

Paratypes. COLOMBIA *Dpto. Magdalena*, Sierra Nevada de Santa Marta: Serra Nueva Granada, 1,620 m, 7 April 1975, ♀; 1,570 m, 28 April 1975, ♀ (J. Kochalka, MCZ). *Valle:* above Saladito, 1,800 m, ♀ (W. Eberhard, no. 965, MCZ).

Chrysometa rubromaculata (Keyserling) Figures 482–486

Tetragnatha rubromaculata Keyserling, 1863: 150, pl. 7, figs. 15, 16, ♀. Female lectotype here designated from New Granada [Spanish colony of Colombia and Panama], (BMNH), examined.

Argyroepeira rubromaculata:—Keyserling, 1893: 332, pl. 17, figs. 245, 245c (not 245b, d, e).

Chrysometa rubromaculata:—Roewer, 1942: 913. Bonnet, 1956: 1083.

Note. The type of this species had been lost. Keyserling reports on two females. A female and male of a similar species marked *A. rubromaculata* were found by Paul Hillyard in the BMNH collections; the female a new species here named *C. keyserlingi* (Keyserling, 1893, fig. 245b), the male *C. alboguttata* (Keyserling, 1893, fig. 245 c, d). The two lost females were in a vial marked *Meta granadensis* Keyserling [nomen nudum], in the Keyserling collection. One of these was used for Keyserling's 1863 figs. 15, 16 and 1893 fig. 245c; the other was another species of *Chrysometa.*

Description. Female. Carapace, sternum, legs yellow. Dorsum of abdomen covered with silver spots (Fig. 486); venter with silver spots on sides and a black band from epigynum to spinnerets, slightly constricted anteriorly. Eyes subequal in size. Anterior median eyes 0.8 diameters apart, their diameter from laterals. Posterior median eyes 0.6 diameters apart, 1.2 diameters from laterals. Abdomen oval. Total length, 5.7 mm. Carapace, 2.1 mm long, 1.7 mm wide. Third patella and tibia, 1.5 mm; fourth, 2.1 mm.

Diagnosis. The diagonal sclerotized anterior border of the transverse bar of the epigynum distinguishes this species (Fig. 484) from others having a short septum.

Chrysometa rincon new species Figures 487–490; Map 3

Holotype. Female from Rincon, Chiapas, Mexico, 6 April 1953 (L. I. Davis, AMNH). The name is a noun in apposition after the type locality.

Description. Female. Carapace light orange with two dusky paraxial bands from posterior median eyes; sternum orange; legs orange with black spots and ringed. Dorsum of abdomen with silver spots and paired dusky patches in two posteriorly converging lines; venter with black band widest in middle and silver spots on each side. Secondary eyes equal to 1.3 diameters of anterior median eyes. Anterior median eyes their diameter apart, same distance from laterals. Posterior median eyes 0.8 diameters apart, slightly more than their diameter from laterals. Abdomen oval. Total length, 5.0 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 3.0 mm; patella and tibia, 3.8 mm; metatarsus, 3.0 mm; tarsus, 1.1 mm. Second patella and tibia, 2.5 mm; third, 1.1 mm; fourth, 1.8 mm.

Diagnosis. The trapezoidal transverse bar having a small anterior lobe on each side of the septum of the epigynum (Fig.

489) distinguishes this species from *C. jelskii* and others.

Chrysometa ludibunda (Keyserling), new combination
Figures 491–496; Map 4

Argyroepeira ludibunda Keyserling, 1893: 352, pl. 18, fig. 260, ♀, ♂. Female lectotype from Monte Verde [Est. Rio de Janeiro], male paralectotype from Cerra Vermelho [Est. Rio de Janeiro], Brazil (BMNH), examined.

Meta ludibunda:—Roewer, 1942: 919. Bonnet, 1957: 2787.

Description. Female. Carapace yellow; sternum with black pigment; legs yellow with indistinct darker marks. Dorsum of abdomen with paired white and gray patches; venter with wide longitudinal black band, light anterior, dark posterior, no white marks. Posterior median eyes 1.2 diameters of anterior medians; lateral eyes equal to 0.9 diameters of anterior median eyes. Anterior median eyes slightly less than their diameter apart, same distance from laterals. Posterior median eyes 0.8 diameters apart, same distance from laterals. Abdomen oval. Total length, 3.8 mm. Carapace, 1.7 mm long, 1.3 mm wide. First femur, 2.4 mm; patella and tibia, 2.7 mm; metatarsus, 2.3 mm; tarsus, 0.9 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm; fourth, 1.7 mm.

Male. Coloration like female. Head reddish brown, otherwise yellow. Dorsum of abdomen with seven pairs of white spots, dark spot anteriorly on sides, posteriorly with pair of gray patches. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, 0.6 diameters from laterals. Posterior median eyes slightly less than their diameter apart, same distance from laterals. Total length, 3.0 mm. Carapace, 1.5 mm long, 1.3 mm wide. First femur, 3.1 mm; patella and tibia, 3.7 mm; metatarsus, 3.2 mm; tarsus, 0.5 mm. Second patella and tibia, 2.4 mm; third, 1.0 mm; fourth, 1.6 mm.

Variation. Recently collected specimens have smaller eyes. This is perhaps due to the presence of dark pigment which is faded in the old Keyserling specimens. Some specimens have black pigment on the abdomen.

Diagnosis. The wide flat transverse bar of the epigynum containing the shadows of a pair of dark triangles (Fig. 493) distinguishes females. Males have a wider tegulum of the palpus than *C. unicolor*, a shorter palpal tibia and a longer "lower" prong of the paracymbium (Figs. 495, 496).

Records. BRAZIL. *Est. Rio de Janeiro:* Teresópolis, 900–1,000 m, March 1946, ♀, imm. (H. Sick, AMNH); Paineiras, Rio de Janeiro, 22 Jan. 1959, ♂ (A. M. Nadler, AMNH). *São Paulo:* Boracéia, 12 Jan. 1961, ♂, 27 Feb. 1967, ♀ (P. Biasi, MZSP).

Chrysometa jelskii new species
Figures 497–500; Map 4

Holotype. Female from Monterico, Dpto. Ayacucho [ca. 12°28'S, 73°54'W], Peru, (K. Jelski, PAN). The species is named after the collector.

Description. Female. Carapace orange with indistinct darker areas and light orange median line; sternum orange; legs orange with indistinct rings. Dorsum and sides of abdomen with silver spots, more than their diameter apart, dark longitudinal band of transverse bars, widest anteriorly. Venter with black band, few silver spots on sides. Eyes subequal in size. Anterior median eyes 0.6 diameters apart, their diameter from laterals. Posterior median eyes 0.7 diameters apart, 1.2 diameters from laterals. Abdomen oval. Total length, 5.5 mm. Carapace, 2.0 mm long, 1.5 mm wide. First femur, 2.8 mm; patella and tibia, 3.3 mm; metatarsus, 3.0 mm; tarsus, 1.1 mm. Second patella and tibia, 2.3 mm; third, 1.2 mm; fourth, 1.9 mm.

Diagnosis. The transverse bar having a slight notch on each side of the short, wide septum (Fig. 499) distinguishes the epigynum of this species from those of *C. rincon* and *C. decolorata*.

Chrysometa decolorata (O. P.-Cambridge), new combination
Figures 501–505; Map 4

Meta decolorata O. P.-Cambridge, 1889: 3, pl. 1, fig. 4, ♀. Female holotype from Guatemala (BMNH), examined.

Pseudometa decolorata:—F. P.-Cambridge, 1903: 446, pl. 42, fig. 22, ♀. Roewer, 1942: 922. Bonnet, 1958: 3817.

Description. Female. Carapace orange-yellow. Sternum, legs with some gray pigment. Dorsum of abdomen with silver spots; venter with two longitudinal lines of silver spots (Fig. 505). Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, slightly more than their diameter from laterals. Posterior median eyes slightly less than their diameter apart, 1.3 diameters from laterals. Abdomen oval. Total length of holotype, 5.9 mm. Carapace, 2.9 mm long, 2.2 mm wide. First femur, 3.2 mm; patella and tibia, 4.0 mm; metatarsus, 3.1 mm; tarsus, 1.3 mm. Second patella and tibia, 3.2 mm; third, 1.6 mm; fourth, 2.7 mm.

Note. Figures 501–505 were made from a recently collected female.

Variation. The recently collected females have slightly longer legs, total length 5.6 mm, carapace 2.4 mm long, 1.8 mm wide, first patella and tibia 4.7 mm.

Diagnosis. The oval transverse bar and indistinct septum of the epigynum (Fig. 503) distinguish this species from related ones.

Record. GUATEMALA *Dpto. Baja Verapaz:* Purulhá, 2,300 m, 22–23 April 1979, 3♀ (J. Coddington, MCZ, USNM).

Chrysometa unicolor (Keyserling), new combination
Figures 506, 507

Meta unicolor Keyserling, 1880: 566, pl. 16, fig. 15, ♂. Male holotype from New Granada (Spanish colony of Colombia and Panama) (BMNH), examined. Roewer, 1942: 920. Bonnet, 1957: 2805.

Argyroepeira unicolor:—Keyserling, 1893: 349, pl. 18, fig. 257, ♂.

Note. The holotype has only a left palpus; it is in poor condition, having been glued to a pinpoint at one time.

Description. Male. Carapace, sternum, legs orange-yellow. Dorsum of abdomen covered by silver spots. Eyes subequal in size. Anterior median eyes their diameter apart, 1.2 diameters from laterals. Posterior median eyes 1.2 diameters apart, 1.5 diameters from laterals. Abdomen oval. Total length, 3.1 mm. Carapace, 1.5 mm long, 1.2 mm wide. First femur, 2.9 mm; patella and tibia, 3.5 mm. Second patella and tibia, 2.1 mm; third, 0.9 mm; fourth, 1.5 mm.

Diagnosis. The male palpus of this species has a narrower tegulum, a longer tibia and a different proximal end of the paracymbium (Figs. 506, 507) than *C. ludibunda.*

Chrysometa craigae new species
Figures 508–514; Map 4

Holotype. Male from Bosque Nuboso, Monteverde Cloud Forest Reserve, 1,580 m el., 25 Feb. 1977,

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Figures 491–496. *Chrysometa ludibunda* (Keyserling). 491–494. Epigynum. 491. Dorsal, cleared. 492. Ventral, cleared. 493. Ventral. 494. Posterior. 495, 496. Left male palpus. 495. Ventral. 496. Lateral.

Figures 497–500. *C. jelskii* n. sp., epigynum. 497. Dorsal, cleared. 498. Ventral, cleared. 499. Ventral. 500. Posterior.

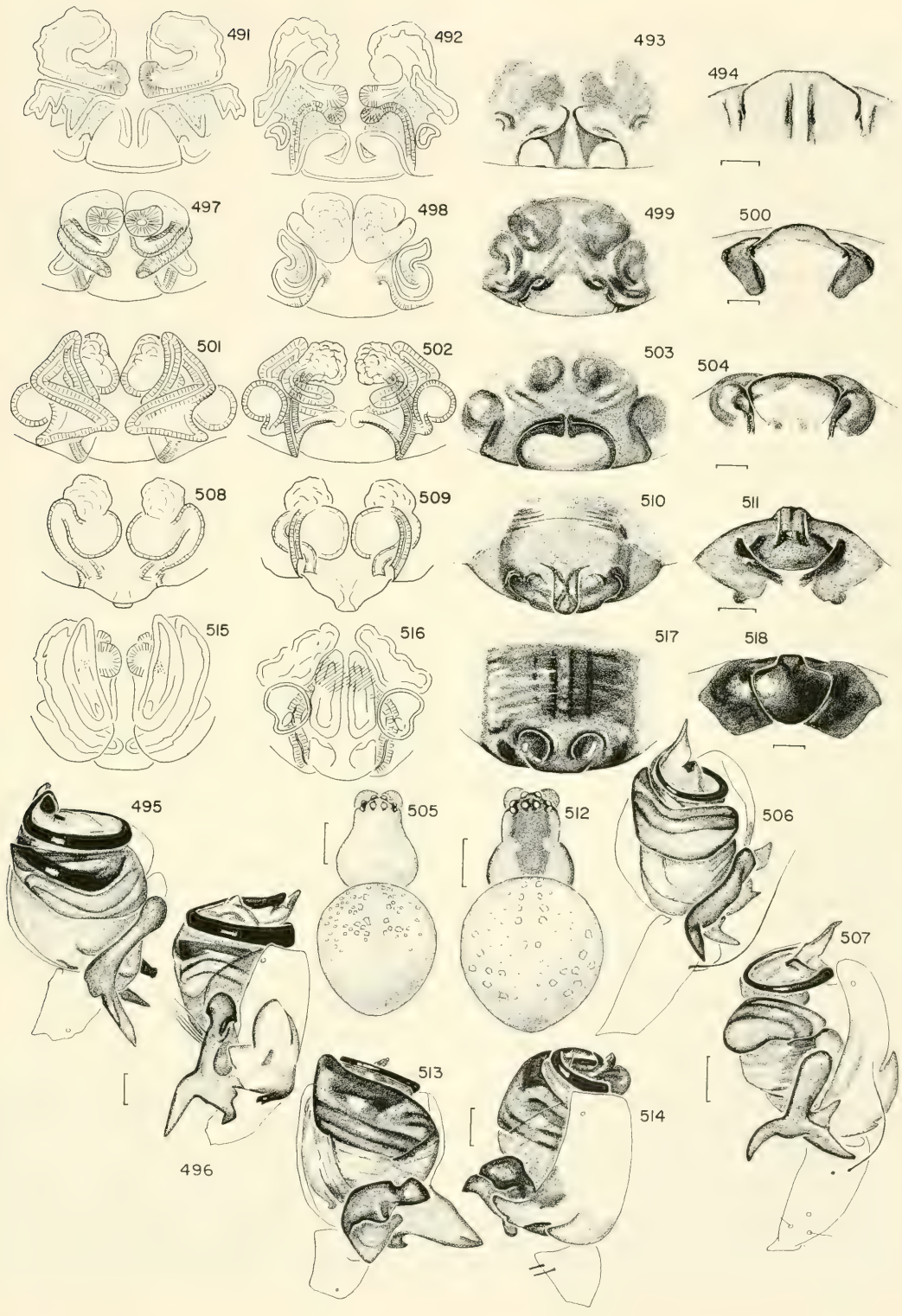
Figures 501–505. *C. decolorata* (O. P.-Cambridge). 501–504. Epigynum. 501. Dorsal, cleared. 502. Ventral, cleared. 503. Ventral. 504. Posterior. 505. Female.

Figures 506, 507. *C. unicolor* (Keyserling), male palpus. 506. Ventral. 507. Lateral.

Figures 508–514. *C. craigae* n. sp. 508–511. Epigynum. 508. Dorsal, cleared. 509. Ventral, cleared. 510. Ventral. 511. Posterior. 512. Female. 513, 514. Male palpus. 513. Ventral. 514. Lateral.

Figures 515–518. *C. machala* n. sp., epigynum. 515. Dorsal, cleared. 516. Ventral, cleared. 517. Ventral. 518. Posterior.

Scale lines. 0.1, except Figures 505, 512, 1.0 mm.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Prov. Puntarenas, Costa Rica (C. L. Craig, MCZ). The species is named after ecologist and collector Cay Craig.

Description. Female. Carapace orange-yellow, head orange; sternum yellow; legs yellow, indistinctly ringed. Dorsum of abdomen with scattered silver spots and two bands of gray marks (Fig. 512); venter with scattered silver spots. Eyes subequal in size. Anterior median eyes 0.8 diameters apart, their diameter from laterals. Posterior median eyes 0.7 diameters apart, 1.2 diameters from laterals. Abdomen oval, evenly rounded. Total length, 4.8 mm. Carapace, 2.4 mm long, 1.7 mm wide. First femur, 3.0 mm; patella and tibia, 3.5 mm; metatarsus, 2.8 mm; tarsus, 1.2 mm. Second patella and tibia, 2.9 mm; third, 1.5 mm; fourth 2.2 mm.

Male. Color markings like female. Eyes subequal in size. Anterior median eyes 0.8 diameters apart, 0.5 from laterals. Posterior median eyes 0.5 diameters apart, 0.8 from laterals. Total length, 3.0 mm. Carapace, 1.4 mm long, 1.2 mm wide. First femur, 2.7 mm; patella and tibia, 3.6 mm; metatarsus, 2.9 mm; tarsus, 1.2 mm. Second patella and tibia, 2.2 mm; third, 1.1 mm; fourth 1.4 mm.

Variation. Females vary in total length from 4.7 to 5.6 mm, males from 3.0 to 4.0 mm.

Diagnosis. The epigynum of this species differs from all others by a median septum above the transverse bar; the bar has a lateral pocket on each side (Figs. 510, 511). On the sides are paraxial dark marks (Fig. 510). The male palpus can be separated from that of other species by the triangular curved projection of the cymbium and the shape of the paracymbium (Figs. 513, 514).

Natural History, Distribution. From forest, 1,500 m, Costa Rica (Map 4).

Paratypes. COSTA RICA *Prov. Puntarenas:* Bosque Pantanosa, Monteverde Cloud Forest, 1,600 m, 23 May 1977, 7 July 1955, 2♂, July 1978, 4♀ (C. L. Craig, P. Klass, MCZ); Bosque del Río, Monteverde Cloud Forest, 24 May 1977, ♂, 4 Aug. 1977, ♀ (C. L. Craig, MCZ); Monteverde Comm. Grindon prop., Powell house, July 1978, ♂ (C. L. Craig, P. Klass, MCZ); swamp forest, Aug. 1977, 4♀ (C. L. Craig, MCZ); Cloud Forest, Monteverde, 1,500 m, 13 July 1980, ♀ (J. Coddington, USNM). *Alajuela:* headwaters of Río Peñas Blancas, 13 July 1980, ♀ (J. Coddington, MCZ). ?*San José:* La Palma, ♀ (J. F. Tristan, MCZ). *Cartago:* Tuis, hilltops, 1 June 1979, ♀ (J. Coddington, MCZ).

Chrysometa machala new species
Figures 515–518; Map 4

Holotype. Female from Buenavista, 20 km SE of Machala, Prov. El Oro, Ecuador, 11 Jan. 1943 (E. L. Moore, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female in poor, shriveled condition. Dorsum of abdomen covered with silver spots; venter with median dark band constricted anteriorly by a pair of light patches of silver spots. Total length, 3.0 mm. Carapace, 1.4 mm long. First femur, 2.3 mm; patella and tibia, 2.9 mm; metatarsus, 2.1 mm; tarsus, 0.9 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 2.0 mm.

Note. In the Keyserling collection (BMNH) is a specimen of this species from Peru; it had been marked *C. opulenta.*

Diagnosis. The short transverse bar and the depressions on each side of the septum, each depression surrounded by a circular lip (Fig. 517), as well as the bulge of the bar in posterior view (Fig. 518) of the epigynum, distinguish this species from *C. itaimba.*

Chrysometa itaimba new species
Figures 519–522; Map 4

Holotype. Female from Itaimbézinho, Cambará do Sul, Est. Rio Grande do Sul, Brazil, 5 Jan. 1985 (A. Lise, MCN no. 12796). The name is an arbitrary combination of letters.

Description. Female. Carapace yellowish with black patch behind posterior median eyes, widening behind head, and coming to point on thorax; chelicerae dark brown; labium, endites blackish brown;

sternum orange; legs yellowish with distinct black rings. Dorsum of abdomen with tiny scattered silver spots, some black marks anteriorly, posterior half with median black band broken in middle; sides with tiny silver spots; venter with rectangular black patch, longer than wide. Anterior lateral eyes equal to diameter of anterior medians; posterior median eyes equal to 0.9 diameters; posterior lateral eyes equal to 0.8 diameters of anterior median eyes. Anterior median eyes 0.6 diameters apart, 0.5 diameters from laterals. Posterior median eyes slightly less than their diameter apart, slightly more than their diameter from laterals. Abdomen spherical. Total length, 5.0 mm. Carapace, 2.2 mm long, 1.7 mm wide. First femur, 3.1 mm; patella and tibia, 3.7 mm; metatarsus, 2.9 mm; tarsus, 1.1 mm. Second patella and tibia, 2.6 mm; third, 1.2 mm; fourth, 1.9 mm.

Diagnosis. The shape of the septum and transverse bar and the comma-shaped depressions on each side of the septum of the epigynum (Fig. 521) distinguish this species from *C. machala.*

Natural History, Distribution. Found at low elevations, southeastern Brazil (Map 4).

Paratype. BRAZIL *Est. São Paulo:* Campos do Jordão, 3 Jan. 1948, ♀ (F. Lane, MZSP).

Chrysometa nigrovittata Keyserling, new combination

Figures 523–529; Map 4

Meta nigrovittata Keyserling, 1865: 833, pl. 20, figs. 1–3, ♂. Male holotype from New Granada [Spanish colony of Colombia and Panama] (BMNH), examined. Roewer, 1942: 919. Bonnet, 1957: 2796.

Note. A juvenile female is with type male in the vial.

Description. Female. Carapace, legs orange-yellow; sternum orange, sides gray. Dorsum of abdomen with large silver spots, posterior with median dark band (Fig. 527); sides with silver spots; sides of venter with longitudinal lines containing small silver spots, ending in a large silver spot some distance in front of spinnerets. Lateral eyes equal to 1.3 diameters of anterior medians; posterior median eyes equal to 1.4 diameters of anterior medians. Anterior median eyes slightly more than their diameter apart, 1.5 diameters from laterals. Posterior median eyes slightly less than their diameter apart, 1.5 diameters from laterals. Abdomen oval. Total length, 6.0 mm. Carapace, 2.2 mm long, 1.8 mm wide. First femur, 3.2 mm; patella and tibia, 4.2 mm; metatarsus, 3.4 mm; tarsus, 1.4 mm. Second patella and tibia, 2.7 mm; third, 1.4 mm; fourth, 2.2 mm.

Male holotype. Carapace yellow-white; darker streaks from thoracic grooves to posterior median eyes and to sides of eyes. Chelicerae brown. Sternum yellow. Legs yellow with indistinct darker patches. Dorsum of abdomen with three pairs of silver patches on anterior, and on each side a longitudinal silver band, posteriorly transverse black marks; venter black with a pair of silver patches, indistinct silver lines of tiny dots. Secondary eyes 1.2 diameters of anterior medians. Anterior median eyes slightly more than their diameter apart, 1.4 from laterals. Posterior median eyes slightly less than their diameter apart, 1.3 from laterals. Abdomen suboval. Total length, 4.7 mm. Carapace, 2.3 mm long, 1.9 mm wide. First femur, 6.5 mm; patella and tibia, 6.5 mm; metatarsus, 5.2 mm; tarsus, 1.8 mm. Second patella and tibia, 3.5 mm; third, 1.7 mm; fourth, 2.6 mm.

Variation. Females vary in total length from 5.5 to 6.0 mm, males from 4.7 to 5.2 mm.

Diagnosis. The lobes on the anterior margin of the square transverse bar of the epigynum (Fig. 525) distinguish females from *C. itaimba.* The shape of the paracymbium (Figs. 528, 529) distinguishes males.

Natural History, Distribution. 2,900 to 3,100 m, southern Colombia, Ecuador.

Records. COLOMBIA *Dpto. Cauca:* Puracé Natl. Park, path from Cascada San

Nicolas, 2,900 m, 16 Jan. 1983, ♂ (J. Kochalka, MCZ). ECUADOR *Prov. Azuay:* Cerro Tinajillas, 3,100 m, 18–21 March 1965, 10♀, 3♂ (L. Peña, MCZ); 8 km E of Sevilla de Oro, 17 Feb. 1955, ♀ (E. I. Schlinger, E. S. Ross, CAS).

Chrysometa flava (O. P.-Cambridge), new combination
Figures 530–536; Map 4

Meta flava O. P.-Cambridge, 1894: 135, pl. 18, fig. 8, ♂. Male holotype from Teapa, Tabasco, Mexico (BMNH), examined.

Pseudometa flava:—F. P.-Cambridge, 1903: 445, pl. 42, fig. 17, ♂. Roewer, 1942: 922. Bonnet, 1958: 3817.

Description. Female. Carapace, sternum, legs orange-yellow, distal ends of tibiae black. Abdomen with silver spots (Fig. 534), black on venter and on sides of spinnerets, with dark area extending halfway from posterior end to epigynum. Eyes subequal in size except posterior laterals, 0.8 diameters of anterior medians. Anterior median eyes their diameter apart, 1.2 diameters from laterals. Posterior median eyes 0.9 diameters apart, 1.2 diameters from laterals. Total length, 5.7 mm. Carapace, 2.9 mm long, 2.1 mm wide. First femur, 3.7 mm; patella and tibia, 4.4 mm; metatarsus, 3.5 mm; tarsus, 1.4 mm. Second patella and tibia, 3.7 mm; third, 1.7 mm; fourth, 2.9 mm.

Male. Coloration, eyes similar to female. Total length, 4.4 mm. Carapace, 2.3 mm long, 1.9 mm wide. First femur, 4.2 mm; patella and tibia, 4.9 mm; metatarsus, 4.3 mm; tarsus, 1.3 mm. Second patella and tibia, 3.8 mm; third, 1.5 mm; fourth, 2.7 mm.

Variation. Total length of females varies from 4.5 mm (Manaus) to 6.1 mm, males from 3.9 to 4.9 mm.

Diagnosis. Chrysometa flava has longer legs than the sympatric *C. heredia.* The oval transverse bar and notched anterior rim of the opening on each side of the narrow septum of the epigynum (Fig. 532) distinguish females; the paracymbium of the palpus having an "up" facing lateral hook (Figs. 535, 536) distinguishes males.

Natural History, Distribution. Found in low elevation forest from southern Mexico to the Amazon.

Records. COSTA RICA *Prov. Heredia:* La Selva near Puerto Viejo, very common, ♀♀, ♂♂ (AMNH, MCZ, MZCR). *Cartago:* Turrialba, 15 Aug. 1963, ♀ (W. Peck, EPC). BRAZIL *Est. Amazonas:* Res. Ducke, Manaus, Aug. 1971, ♀ (M. E. Galiano, MG).

Chrysometa buenaventura new species
Figures 537–541; Map 4

Holotype. Female from 28 km east of Buenaventura, 50 m el., Dpto. Valle, Colombia, 1977 (W. Eberhard, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellowish with brown pattern, chelicerae brown

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Figures 519–522. *Chrysometa itaimba* n. sp., epigynum. 519. Dorsal, cleared. 520. Ventral, cleared. 521. Ventral. 522. Posterior.

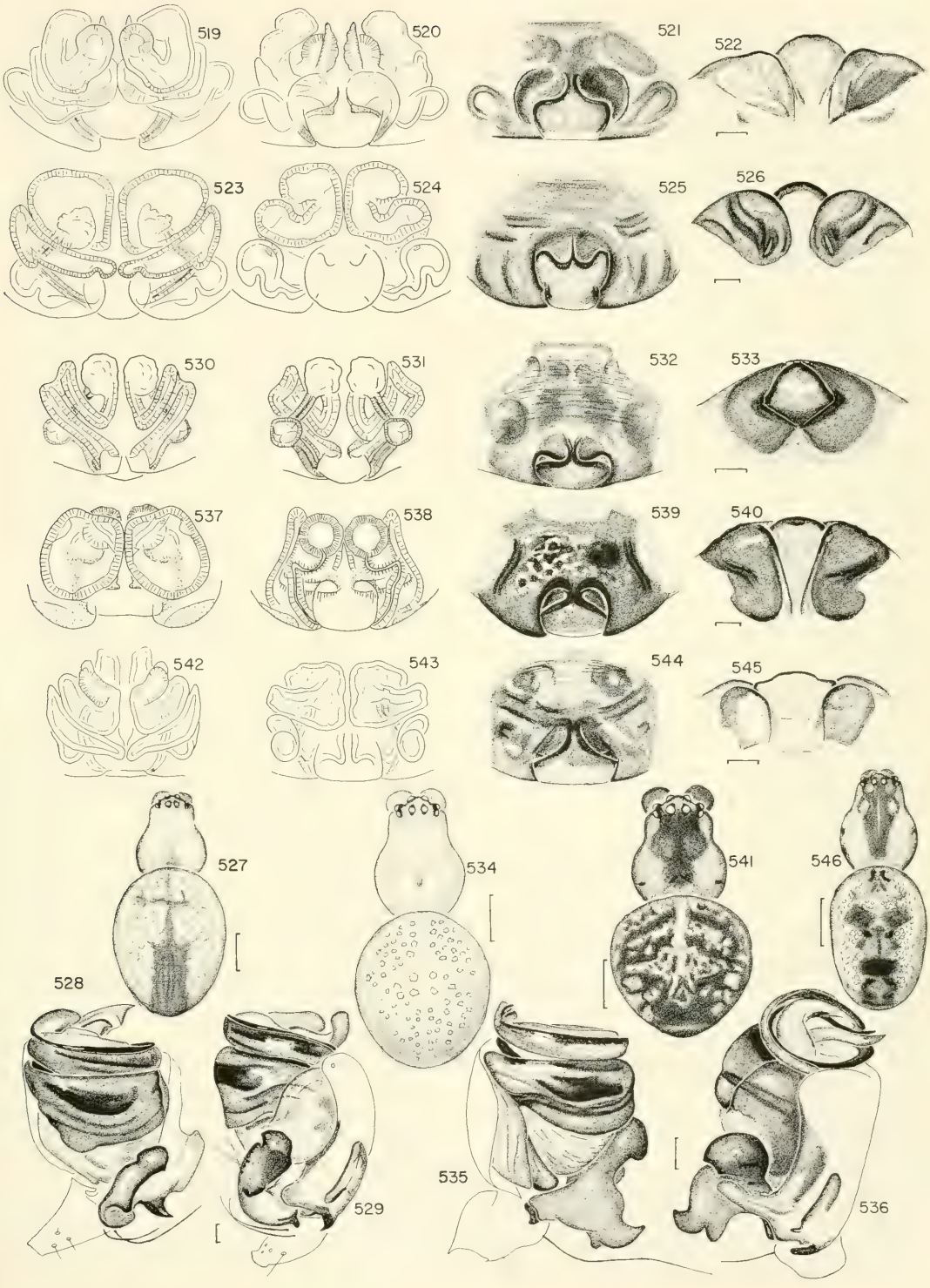
Figures 523–529. *C. nigrovittata* (Keyserling). 523–526. Epigynum. 523. Dorsal, cleared. 524. Ventral, cleared. 525. Ventral. 526. Posterior. 527. Female. 528, 529. Left male palpus. 528. Ventral. 529. Lateral.

Figures 530–536. *C. flava* (O. P.-Cambridge). 530–533. Epigynum. 530. Dorsal, cleared. 531. Ventral, cleared. 532. Ventral. 533. Posterior. 534. Female. 535, 536. Male palpus. 535. Ventral. 536. Lateral.

Figures 537–541. *C. buenaventura* n. sp. 537–540. Epigynum. 537. Dorsal, cleared. 538. Ventral, cleared. 539. Ventral. 540. Posterior. 541. Female.

Figures 542–546. *C. claudia* n. sp. 542–545. Epigynum. 542. Dorsal, cleared. 543. Ventral, cleared. 544. Ventral. 545. Posterior. 546. Female.

Scale lines. 0.1 mm, except Figures 527, 534, 541, 546, 1.0 mm.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(Fig. 541); sternum brown; legs ringed brown on yellow. Abdomen with gray pattern (Fig. 541), few tiny silver spots; sides with gray streaks; venter black with two longitudinal light lines. Eyes subequal in size. Anterior medians 0.5 diameters apart, same distance from laterals. Posterior median eyes 0.5 diameters apart, their diameter from laterals. Abdomen subspherical, slightly pointed posteriorly. Total length, 4.5 mm. Carapace, 2.4 mm long, 1.9 mm wide. First femur, 3.0 mm; patella and tibia, 3.6 mm; metatarsus, 2.4 mm; tarsus, 1.1 mm. Second patella and tibia, 2.6 mm; third, 1.4 mm; fourth, 2.1 mm.

Variation. Total length of females varies from 4.3 to 5.4 mm.

Diagnosis. The lateral lips of the depression that overhang the septum anteriorly and the slightly punctate area anterior of the sculpturing of the epigynum (Fig. 539), distinguish this species from *C. flava.*

Paratypes. COLOMBIA *Dpto. Valle:* Cent. Hid. del Río Anchicayá, 400 m, ♀ (W. Eberhard, MCZ); Río Digua near Queremal, 19 June 1976, ♀ (W. Eberhard, no. 284, MCZ).

Chrysometa claudia new species
Figures 542–546; Map 4

Holotype. Female from parama San José, between Las Gonzalez and La Mucutuy, 3,000 m, Est. Mérida, Venezuela, 13 Oct. 1984 (C. Sobrevila, USNM). The species is named after the collector.

Description. Female. Carapace whitish with brown marks on head and rim of thorax (Fig. 546); sternum with brownish sides; legs with dark rings. Dorsum of abdomen with brown scalloped-edged median band containing a black patch, silver spots to sides (Figs. 546); sides with scattered silver spots; venter with brownish band containing pair of black marks closer to spinnerets than to epigynum, with line of silver spots on each side. Anterior lateral eyes, posterior median eyes equal to 1.5 diameters of anterior medians; posterior lateral eyes equal to 1.3 diameters of anterior median eyes. Anterior median eyes slightly more than their diameter apart, 1.5 diameters from laterals. Posterior median eyes 0.6 diameters apart, 1.2 diameters from laterals. Abdomen elongate oval. Total length, 5.0 mm. Carapace, 2.1 mm long, 1.5 mm wide. First femur, 3.2 mm; patella and tibia, 3.9 mm; metatarsus, 3.4 mm; tarsus, 1.3 mm. Second patella and tibia, 2.6 mm; third, 1.3 mm; fourth, 2.1 mm.

Diagnosis. The even curvature of the concave rims of septum and transverse bar of the epigynum (Fig. 544) distinguish this species from others.

Chrysometa cebolleta new species
Figures 547–553; Map 4

Holotype. Female from Río Donachui, 3,000 m, Sierra Nevada de Santa Marta, Colombia, 19 Jan. 1974 (J. A. Kochalka, MCZ). The specific name is a noun in apposition after a collecting locality.

Description. Female. Carapace yellow with contrasting marks (Fig. 551). Sternum banded in black on each side, orange-yellow in middle; bands of equal width. Legs ringed and spotted. Dorsum of abdomen contrastingly marked (Fig. 551), without silver spots; venter with a black band, posterior third of band constricted by a light colorless patch on each side. Lateral eyes equal to diameter of anterior median eyes; posterior median eyes 1.2 diameters of anterior medians. Anterior median eyes slightly less than their diameter apart, 1.7 diameters from laterals. Posterior median eyes 0.7 diameters apart, 1.5 diameters from laterals. Abdomen elongate oval. Total length, 7.0 mm. Carapace, 3.2 mm long, 2.5 mm wide. First femur, 5.9 mm; patella and tibia, 6.5 mm; metatarsus, 5.2 mm; tarsus, 1.6 mm. Second patella and tibia, 4.2 mm; third, 2.1 mm; fourth, 3.2 mm.

Male. Carapace markings less distinct than those of female. Eyes subequal in size. Anterior median eyes their diameter apart, 1.5 diameters from laterals. Posterior median eyes slightly less than their diameter apart, 1.3 diameters from laterals. Total

length, 4.5 mm. Carapace, 2.0 mm long, 1.7 mm wide. First femur, 4.4 mm; patella and tibia, 5.5 mm; metatarsus, 5.5 mm; tarsus, 1.6 mm. Second patella and tibia, 3.2 mm; third, 1.3 mm; fourth, 2.2 mm.

Diagnosis. The swollen anterior of the septum and the squarish transverse bar, together with the paired dark patches of the epigynum (Fig. 549), distinguish females. The tighter coiled conductor and embolus of the palpus (Figs. 552, 553) separate males from *C. nigrovittata.*

Paratypes. COLOMBIA *Dept. Magdalena*, Sierra Nevada de Santa Marta: Río Donachui Trail, 2,400–2,800 m, 2 Jan. 1973, ♀ (J. A. Kochalka, MCZ); Casa Antonio, Loma Cebolleta, 2,700 m, 15 Feb. 1974, ♂ (J. A. Kochalka, MCZ).

Chrysometa guttata (Keyserling), new combination

Figures 554–560; Map 4

Zilla guttata Keyserling, 1881: 30:551, pl. 16, fig. 3, ♀. Female holotype from Amable Maria [Dpto. Junín] Peru, (PAN), examined.

Araneus gemellus:—Petrunkevitch, 1911: 293. New name for *Zilla guttata,* not *Epeira guttata* Keyserling.

Zygiella guttata:—Roewer, 1942: 887. Bonnet, 1959: 5002.

Capichameta ribeiroi Soares and Camargo, 1955: 574, fig. 6, ♂. Male holotype from Rio São José, Município de Colatina, Est. Espírito Santo, Brazil (MZSP), examined. NEW SYNONYMY.

Description. Female. Carapace, legs yellow; sternum grayish yellow. Dorsum of abdomen with silver spots spaced more than their diameter apart (Fig. 558); venter blackish on each side with pigmentless patch containing silver spots, extending from epigynum halfway to spinnerets; black ring around spinnerets, broken dorsally. Secondary eyes 1.3 diameters of anterior median eyes. Anterior median eyes slightly more than their diameter apart, their diameter from laterals. Posterior median eyes 0.8 diameters apart, their diameter from laterals. Abdomen oval. Total length, 4.7 mm. Carapace, 2.2 mm long, 1.7 mm wide. First femur, 2.7 mm; patella and tibia, 3.2 mm; metatarsus, 2.5 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.3 mm; fourth, 2.1 mm.

Male. Coloration like female. Posterior median eyes equal to diameter of anterior medians; lateral eyes 0.8 diameters of anterior median eyes. Anterior median eyes slightly less than their diameter apart, 0.3 diameters from laterals. Posterior median eyes 0.3 diameters apart, their diameter from laterals. Total length, 4.2 mm. Carapace, 2.3 mm long, 1.9 mm wide. First femur, 3.8 mm; patella and tibia, 4.3 mm; metatarsus, 3.8 mm; tarsus, 1.3 mm. Second patella and tibia, 3.4 mm; third, 1.4 mm; fourth, 2.3 mm.

Variation. Total length of females varies from 4.2 to 4.8 mm, of males from 3.7 to 4.2 mm.

Diagnosis. The epigynum is distinguished from others by a lateral, longitudinal lip that covers each end of the transverse bar and also encloses a small round opening and by a V-shaped dark mark anterior of the septum (Fig. 556). The paracymbium of the male palpus with a bifid "lower" prong (Figs. 559, 560) distinguishes the male.

Natural History, Distribution. Found in intermediate and low altitude forest, Amazon area (Map 4).

Records. VENEZUELA *Est. Aragua:* Rancho Grande, March 1946, ♀ (W. Beebe, AMNH). COLOMBIA *Dpto. Meta:* 5 km W of Villavicencio, 11 March 1955, ♂ (E. I. Schlinger, E. S. Ross, CAS). *Putumayo:* Río Putumayo nr. Pto. Asis, ♀ (W. Eberhard, no. 448, MCZ). PERU *Dpto. San Martín:* Mishqui-yacu, 20 km NE Moyobamba, 1,600 m, Aug. 1947, ♀ (F. Woytkowski, AMNH). *Huánuco:* Monson Valley, Tingo María, 1954, 4♀, 2♂ (E. I. Schlinger, E. S. Ross, CAS); Tingo María, sev. coll., ♀♀, ♂♂ (AMNH). BRAZIL *Est. Amazonas:* Reserva Ducke, Manaus, Aug. 1971, ♀ (M. E. Galiano, MG). *Mato Grosso:* 260 km N Xavantina, 12°49′S, 51°46′W, 400 m, gallery forest, Feb.–Apr. 1969, ♂ (Xavantina-Cachimpo Exped., MCZ).

Chrysometa alboguttata (O. P.-Cambridge)
Figures 561–567; Map 4

Meta alboguttata O. P.-Cambridge, 1889: 2, pl. 1, figs. 1, 2, ♀, ♂. One female holotype, six female paratypes without locality data (BMNH), examined. Syntypes, according to O. P.-Cambridge, came from San Marcos, Tamahú, Panzós and Sakiyac, Guatemala and Bugaba, Panama.

Argyroepeira alboguttata:—Keyserling, 1893: 317, pl. 16, fig. 233, ♀, ♂.

Argyroepeira rubromaculata:—Keyserling, 1893: 332, pl. 17, figs. 245d, e, ♂, not female. Not *Tetragnatha rubromaculata* Keyserling, 1863.

Meta superans O. P.-Cambridge, 1896: 217, pl. 28, fig. 2, ♂. Two male syntypes from Teapa, Tabasco, Mexico (BMNH), examined. NEW SYNONYMY.

Chrysometa alboguttata:—Banks, 1898: 258.

Pseudometa superans:—F. P.-Cambridge, 1903: 445, pl. 42, fig. 18, ♂. Roewer, 1942, 1: 922. Bonnet, 1958: 3818.

Pseudometa alboguttata:—F. P.-Cambridge, 1903: 446, pl. 42, fig. 21, ♀. Roewer, 1942: 922. Bonnet, 1958: 3817.

Note. Meta superans is the male of *C. alboguttata.*

Description. Female. Carapace, sternum, legs yellow. Distal end of chelicerae and fang brown. Dorsum and sides of abdomen with small silver spots about their diameter apart (Fig. 565). On venter, a pair of longitudinal lines of silver spots, distinct anteriorly, fading out posteriorly. Posterior median eyes 1.2 diameters of anterior medians; both laterals same diameter as anterior medians. Anterior median eyes slightly more than their diameter apart, their diameter from laterals. Posterior median eye slightly less than their diameter apart, their diameter from laterals. Abdomen slightly longer than wide. Total length, 4.1 mm. Carapace, 1.7 mm long, 1.4 mm wide. First femur, 2.2 mm; patella and tibia, 2.7 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 2.0 mm; third, 1.2 mm; fourth, 1.7 mm.

Male. Carapace yellowish with a dark arrow pointing anteriorly in thoracic depression. Sternum, legs yellowish. Dorsum of abdomen with white spots. Secondary eyes slightly larger than anterior medians. Anterior median eyes slightly more than their diameter apart, 0.8 diameters from laterals. Posterior median eyes 0.7 diameters apart, their diameter from laterals. Total length, 3.5 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 2.9 mm; patella and tibia, 3.5 mm; metatarsus, 2.7 mm; tarsus, 1.1 mm. Second patella and tibia, 2.7 mm; third, 1.2 mm; fourth, 1.8 mm.

Note. The descriptions were made from the type specimens of *alboguttata* and *superans.*

Variation. Total length of females varied from 3.5 to 5.2 mm, of males from 2.9 to 4.6 mm.

Diagnosis. The epigynum is distinguished by the concave, parallel sides of the septum, the transverse bar having lateral anterior lobes. The openings anterior of the lobes and the distribution of the dark patches around the sculpturing are diagnostic (Fig. 563). The male palpus has a distinct paracymbium whose proximal end is biforked, the "upper" fork pointing "down" in ventral view (Fig. 566), pointing ventrally in lateral view (Fig. 567).

Natural History, Distribution. This is a low altitude to 1,300 m probably rain forest species. One record is from a cave. Mexico to Colombia (Map 4).

Records. MEXICO *Est. Tamaulipas:*

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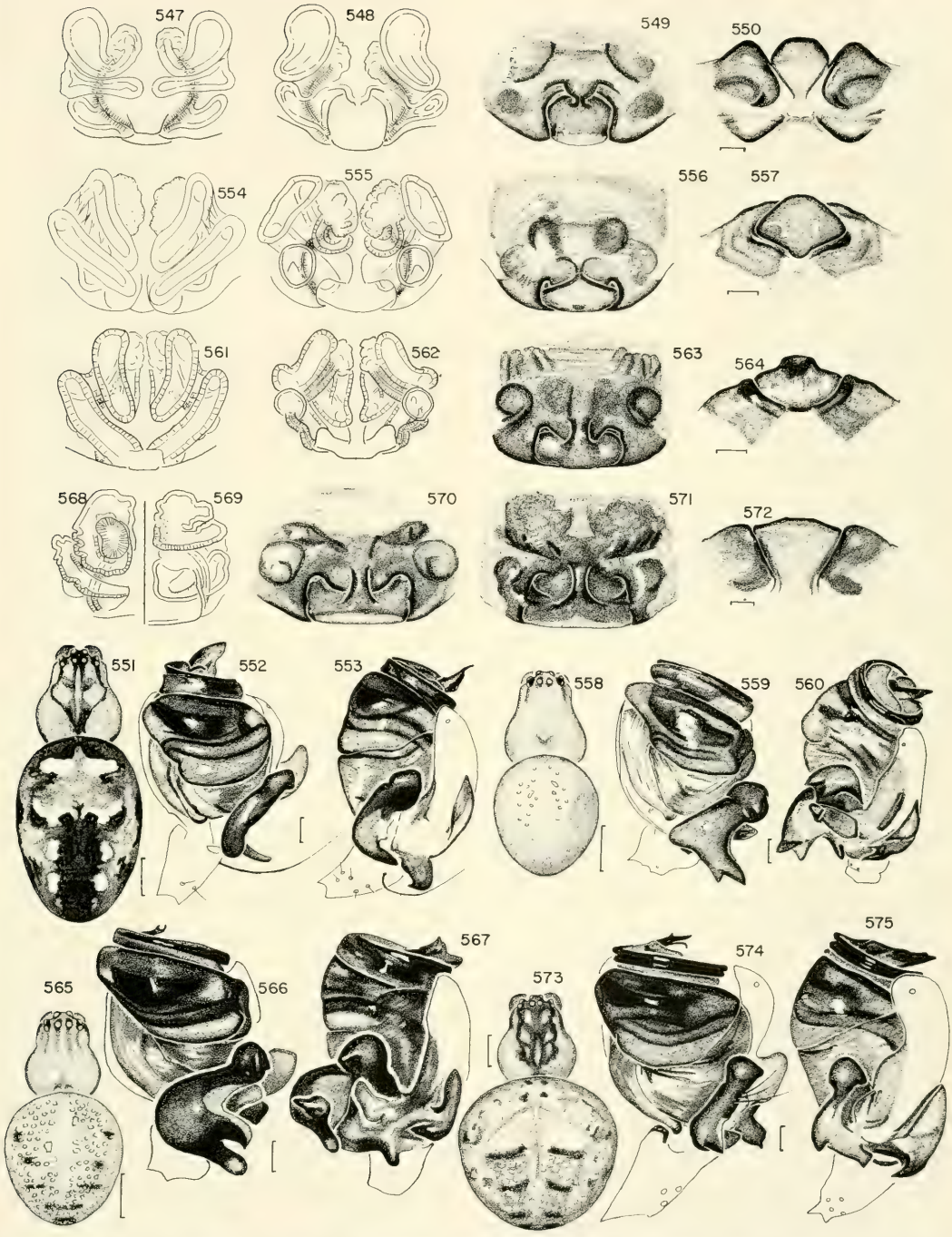
Figures 547–553. *Chrysometa cebolleta* n. sp. 547–550. Epigynum. 547. Dorsal, cleared. 548. Ventral, cleared. 549. Ventral. 550. Posterior. 551. Female. 552, 553. Left male palpus. 552. Ventral. 553. Lateral.

Figures 554–560. *C. guttata* (Keyserling). 554–557. Epigynum. 554. Dorsal, cleared. 555. Ventral, cleared. 556. Ventral. 557. Posterior. 558. Female. 559, 560. Male palpus. 559. Ventral. 560. Lateral.

Figures 561–567. *C. alboguttata* (O. P.–Cambridge). 561–564. Epigynum. 561. Dorsal, cleared. 562. Ventral, cleared. 563. Ventral. 564. Posterior. 565. Female. 566, 567. Male palpus. 566. Ventral. 567. Lateral.



Figures 568–575. *C. boraceia* n. sp. 568–571. Epigynum. 568. Dorsal, cleared. 569. Ventral, cleared. 570, 571. Ventral. 572. Posterior. 573. Female. 574, 575. Male palpus. 574. Ventral. 575. Lateral.

Scale lines. 0.1 mm, except Figures 551, 558, 565, 573, 1.0 mm.

Bee Cave, 8 km N of Chamal, 10 Apr. 1966, ♀ (J. Fish, AMNH). *San Luis Potosí:* Tamazunchale, ♀ (AMNH); 10 km S of Valles, ♀ (AMNH); Río Frio, ♂ (AMNH). *Sinaloa:* 3 km N of Piaxtla, ♀ (AMNH). *Nayarit:* 16 km SE of Tepic, ♀ (AMNH); Tepic, ♀ (AMNH); Compostela, 3♀ (AMNH). *Veracruz:* Martinez de la Torre, ♀ (AMNH); Lago Catemago, 3♂ (RL); near La Palma, ♀, ♂ (MCZ). *Guerrero:* Taxco, ♀ (AMNH). *Tabasco:* Teapa, ♀, ♂ (AMNH). *Chiapas:* La Zacualpa, ♀ (AMNH); Palenque ruins, ♀ (AMNH).

HONDURAS La Ceiba, ♂ (AMNH). COSTA RICA *Prov. San José:* San Isidro del General, 650–1,300 m, 4♀ (MCZ). *Cartago:* Turrialba, 2♀, ♂ (AMNH, MCZ). *Puntarenas:* 6 km S of San Vito, ♂ (MCZ). PANAMA *Prov. Bocas del Toro:* Bugaba, 5♂ (BMNH). *Chiriquí:* Boquete, ♀ (MCZ). *Panamá:* Pipeline Rd., ♀ (MCZ); Summit, ♀ (AMNH); Cocoli, ♂ (AMNH); Barro Colorado Isl., Gatun Lk., ♀ (CUC, AMNH).

COLOMBIA *Dpto. Magdalena,* Sierra Nevada de Santa Marta: San Pedro, 1,100–1,200 m, 3♀, 2♂ (IBNA, MCZ, USNM); above Minca Vall., 800 m, ♀ (IBNA); Río Frio, 500 m, 2♀ (USNM). *Bogotá:* Bogotá, ♂ (BMNH). Valle: many collections near Cali, 800 to 1,300 m (MCZ). ECUADOR *Prov. Los Ríos:* Juan Montalvo, ♂ (AMNH). Balzapamba, 700 m, ♂ (AMNH).

Chrysometa boraceia new species
Figures 568–575; Map 4

Holotype. Female holotype and one female paratype from Boracéia, [Salesópolis], Est. São Paulo, Brazil (MZSP). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange-yellow with brown patches (Fig. 573); chelicerae, sternum orange-brown; legs orange-yellow with brown rings. Dorsum of abdomen with transverse black marks and white pigment spots (Fig. 573); venter with pair of white patches behind epigastric groove and a white longitudinal line on each side. Eyes subequal in size. Anterior median eyes their diameter apart, 0.7 diameters from laterals. Posterior median eyes 0.6 diameters apart, 1.3 diameters from laterals. Clypeus height 0.5 diameters of anterior median eyes. Abdomen spherical. Total length, 7.4 mm. Carapace, 3.1 mm long, 2.5 mm wide. First femur, 4.4 mm; patella and tibia, 5.5 mm; metatarsus, 3.6 mm; tarsus, 1.1 mm. Second patella and tibia, 3.9 mm; third, 1.9 mm; fourth, 2.9 mm.

Male. Coloration like female. Eyes subequal in size. Anterior median eyes their diameter apart, 0.4 diameters from laterals. Posterior median eyes 0.6 diameters apart, 1.2 diameters from laterals. Abdomen oval. Total length, 4.8 mm. Carapace, 2.4 mm long, 2.0 mm wide. First femur, 5.9 mm; patella and tibia, 7.6 mm; metatarsus, 6.0 mm; tarsus, 1.5 mm. Second patella and tibia, 4.7 mm; third, 1.7 mm; fourth, 2.7 mm.

Variation. The shape of the depressions in the epigynum is variable (Figs. 570, 571). Total length of females varies from 5.4 to 7.4 mm, males from 4.4 to 4.8 mm.

Diagnosis. The epigynum is distinguished by proportions of septum and transverse bar and by the transverse banded dark marks anterior of the depressions (Figs. 570, 571). The male palpus is separated from that of others by the shape of the tip of conductor and embolus and by the shape of the paracymbium and cymbium (Figs. 574, 575).

Natural History, Distribution. Low elevations to 1,600 m, southeastern Brazil (Map 4).

Paratypes. BRAZIL *Est. Rio de Janeiro:* Pico de Tijuca, 500–950 m, 17 April 1965, 4♀ (H. Levi, MCZ); Sumaré, 200–400 m, Feb. 1946, 3♀ (H. Sick, AMNH); Teresópolis, Nov. 1945, ♂, March 1946, 5♀ (H. Sick, AMNH). *São Paulo:* Boracéia, 22–23 Feb. 1961, 2♀ (P. de Biasi, MZSP), Dec. 1949, ♂ (Filho, MZSP), Oct. 1963, ♀ (Oliveira, P. Wygodzinsky, AMNH). *Rio Grande do Sul:* Canela, 11 May 1974, ♀ (A. Lise, MCN); São Francisco di Paula, 23 Jan. 1981, ♀ (A. Lise, MCN); Montenegro, 6 Oct. 1977, ♀ (A. Lise, MCN).

Chrysometa fidelia new species
Figures 576–580; Map 4

Holotype. Female from above Fidelia, 2,000 m, Dept. Valle, Colombia, 2 Dec. 1965 (W. Eberhard, no. 143p, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow with brown markings; sternum brown, lighter in center; coxae yellow; legs ringed brown and yellow. Dorsum of abdomen with pattern of white and brown pigment spots, posteriorly with transverse bars (Fig. 580); venter dark between epigynum and spinnerets, longitudinal white line on each side. Secondary eyes 1.4 diameters of anterior medians. Anterior median eyes 1.2 diameters apart, same distance from laterals. Posterior median eyes 0.8 diameters apart, their diameter from laterals. Total length, 5.3 mm. Carapace, 2.1 mm long, 1.6 mm wide. First femur, 3.2 mm; patella and tibia, 3.8 mm; metatarsus, 2.3 mm; tarsus, 1.1 mm. Second patella and tibia, 2.8 mm; third, 1.3 mm; fourth, 2.0 mm.

Diagnosis. The relative proportions of septum and transverse bar of the epigynum, the lateral oblique lips covering the ends of the bar, and the pattern of the dark patches (Fig. 578) distinguish this species.

Chrysometa brevipes (O. P.-Cambridge), new combination
Figures 581–587; Map 4

Meta brevipes O. P.-Cambridge, 1889: 1, pl. 1, fig. 3, ♀. One female holotype and three female paratypes from Guatemala (BMNH), examined. O. P.-Cambridge cites only a single specimen from Chilascó, Guatemala.

Argyroepeira brevipes:—Keyserling, 1893: 316, pl. 16, fig. 232, ♀.

Pseudometa uncata F. P.-Cambridge, 1903: 445, pl. 42, fig. 19, ♂. Male holotype from Teapa, Tabasco, Mexico (BMNH), examined. NEW SYNONYMY.

Pseudometa brevipes:—F. P.-Cambridge, 1903: 445, pl. 42, fig. 20, ♀. Roewer, 1942: 922. Bonnet, 1958: 3817.

Note. *Pseudometa uncata* is the male of *Chrysometa brevipes*.

Description. Female. Carapace yellowish white, indistinct darker streaks. Sternum orange; legs yellow. Dorsum and sides of abdomen with silver spots; dorsum with transverse gray marks (Fig. 585); venter with longitudinal median gray band; sides with silver spots more dense, forming longitudinal line. Posterior median eyes, anterior lateral eyes 1.5 diameters of anterior medians; posterior lateral eyes 1.3 diameters of anterior medians. Anterior median eyes their diameter apart, 2 diameters from laterals. Posterior median eyes slightly less than their diameter apart, their diameter from laterals. Abdomen spherical. Total length, 4.6 mm. Carapace, 1.8 mm long, 1.4 mm wide. First femur, 2.2 mm; patella and tibia, 2.7 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm; fourth, 1.9 mm.

Male. Carapace light brown; sternum brownish, dark around margin; legs yellow-white. Dorsum and sides of abdomen with silver spots. Dorsum with faint indication of black folium with at least 3 transverse lines posteriorly; venter without pigment. Secondary eyes approximately 1.3 diameters of anterior median eyes. Anterior median eyes more than their diameter apart, 1.4 diameters from laterals. Posterior median eyes their diameter apart, 1.2 diameters from laterals. Total length, 3.5 mm. Carapace, 1.6 mm long, 1.3 mm wide. First femur, 2.6 mm; patella and tibia, 3.0 mm; metatarsus, 2.9 mm; tarsus, 0.9 mm. Second patella and tibia, 2.0 mm; third, 0.9 mm; fourth, 1.4 mm.

Variation. Total length of females varied from 3.4 to 5.1 mm, of males from 3.0 to 4.2 mm.

Diagnosis. Females can be distinguished from other sympatric species by the ventral markings of the abdomen: the two white bands together are wider than the intermediate black area. The depression of the epigynum is bordered by three lips making a diagnostic rectangular depression on each side anterior of the

transverse bar (Fig. 583). The male palpus is distinguished by two loops of the embolus above the tegulum (Figs. 586, 587) and by the almost circular paracymbium with a basal thumb in lateral view (Fig. 587).

Natural History, Distribution. Specimens were collected in oak and agave of cleared forest, in pine forest, oak-pine forest up to 3,000 m altitude from central Mexico to Guatemala (Map 4).

Records. MEXICO *Distrito Federal:* Contreras, 2,500–2,700 m, 30 May 1946, ♀ (AMNH), 23 July 1947, 2♀ (AMNH); Santa Rosa, 24 July 1947, ♀ (AMNH). *Mexico:* Mt. Toluca, ♀ (AMNH), San Francisco Oxtotilpan, ♀, ♂ (MCZ). *Michoacan:* Monte de Zacapu, 2,500 m, 24 Aug. 1959, ♀ (AMNH). *Puebla:* Río Frio, 3,000 m, 26 April 1942, ♀, ♂ (AMNH); summit SW of Río Frio, 2 Aug. 1966, ♀ (AMNH). *Morelos:* Coajomulco, 7 June 1946, ♀ (AMNH). *Oaxaca:* 48 km SW of Valle Nacional, 28 June 1983, ♀ (MCZ). *Chiapas:* nr. San Cristobal, July 1983, 5♀, ♂ (MCZ); July 1950, 2♀ (AMNH).

Chrysometa digua new species
Figures 588–592; Map 4

Holotype. Female from Río San Juan, at mouth of Río Digua, near El Queremal, 1,300 m, Dpto. Valle, Colombia, 1976 (W. Eberhard, MCZ). The specific name is a noun in apposition after the name of the river.

Description. Female. Carapace, sternum, legs orange-yellow; legs darker orange toward distal ends. Dorsum of abdomen with silver spots and paired gray marks (Fig. 592); venter with two longitudinal lines of silver spots. Anterior lateral eyes, posterior median eyes equal to diameter of anterior medians; posterior laterals 0.8 diameters of anterior median eyes. Anterior median eyes 0.8 diameters apart, 0.6 diameters from laterals. Posterior median eyes 0.8 diameters apart, 1.3 from laterals. Abdomen oval. Total length, 5.0 mm. Carapace, 2.3 mm long, 1.7 mm wide. First femur, 3.2 mm; patella and tibia, 4.0 mm; metatarsus, 3.5 mm; tarsus 1.3 mm. Second patella and tibia, 2.8 mm; third, 1.5 mm; fourth, 2.0 mm.

Variation. Total length of female varies from 4.7 to 5.8 mm.

Diagnosis. The epigynum of this species can be distinguished by the two diagonal lips anterior of the openings and by the proportions of septum and transverse bar (Fig. 590).

Paratypes. COLOMBIA *Dpto. Valle:* Cent. Hid. del Río Anchicayá, 400 m, 3♀ (W. Eberhard, nos. 861, 1249, MCZ); road to Anchicayá, 900 m, Nov. 1973, ♀ (W. Eberhard, no. 648, MCZ).

Chrysometa poas new species
Figures 593–600; Map 4

Holotype. Female holotype with 4 immature paratypes from cloud forest around rim of Volcan Poás, 2,500 m, Alajuela Prov., Costa Rica, 27 July 1983

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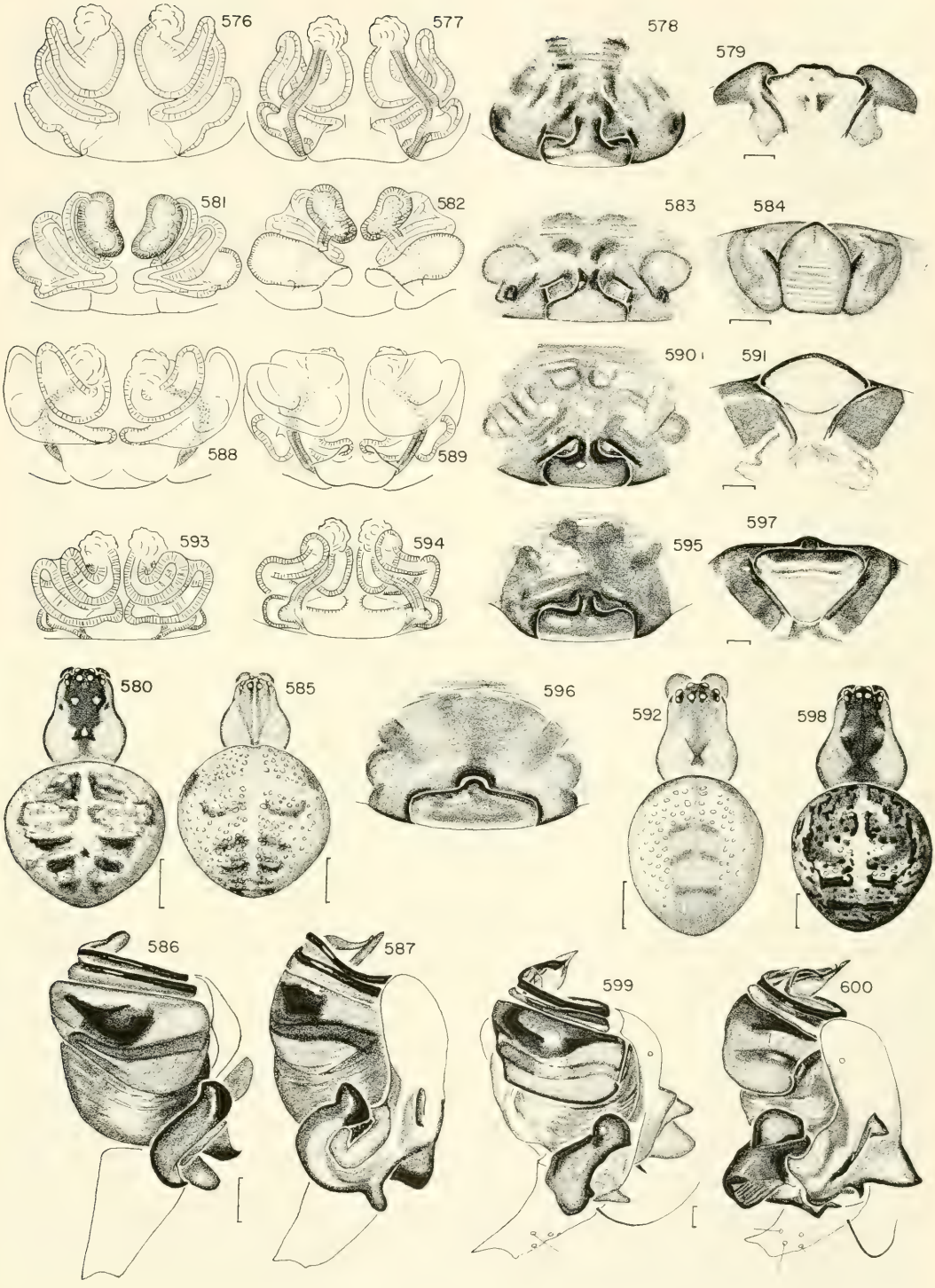
Figures 576–580. *Chrysometa fidelia* n. sp. 576–579. Epigynum. 576. Dorsal, cleared. 577. Ventral, cleared. 578. Ventral. 579. Posterior. 580. Female.

Figures 581–587. *C. brevipes* (O. P.-Cambridge). 581–584. Epigynum. 581. Dorsal, cleared. 582. Ventral, cleared. 583. Ventral. 584. Posterior. 585. Female. 586, 587. Left male palpus. 586. Ventral. 587. Lateral.

Figures 588–592. *C. digua* n. sp. 588–591. Epigynum. 588. Dorsal, cleared. 589. Ventral, cleared. 590. Ventral. 591. Posterior. 592. Female.

Figures 593–600. *C. poas* n. sp. 593–597. Epigynum. 593. Dorsal, cleared. 594. Ventral, cleared. 595, 596. Ventral. 595. (Holotype). 597. Posterior. 598. Female. 599, 600. Male palpus. 599. Ventral. 600. Lateral.

Scale lines. 0.1 mm, except Figures 580, 585, 592, 598, 1.0 mm.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(H., L. Levi, W. Eberhard, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellowish brown with black pattern (Fig. 598). Chelicerae orange-brown; sternum brown; coxae yellow; legs contrastingly ringed. Dorsum of abdomen with black mark surrounded by rusty patches, only a few silver spots; venter with square black mark with a line of silver spots on each side. Eyes subequal in size. Anterior median eyes 0.7 diameters apart, 0.7 diameters from laterals. Posterior median eyes 0.7 diameters apart, 1.3 diameters from laterals. Total length, 7.5 mm. Carapace, 3.6 mm long, 2.7 mm wide. First femur, 5.2 mm; patella and tibia, 6.7 mm; metatarsus, 5.4 mm; tarsus, 1.8 mm. Second patella and tibia, 4.8 mm; third, 2.7 mm; fourth, 3.8 mm.

Male from Cerro de la Muerte. Coloration like female. Eyes subequal in size. Anterior median eyes 0.8 diameters apart, their diameter from laterals. Posterior median eyes 0.8 diameters apart, 1.3 diameters from laterals. Total length, 7.1 mm. Carapace, 3.9 mm long, 3.0 mm wide. First femur, 9.0 mm; patella and tibia, 12.1 mm; metatarsus, 12.8 mm; tarsus, 2.5 mm. Second patella and tibia, 8.2 mm; third, 3.5 mm; fourth, 5.1 mm.

Variation. The females have a similar appearance but there seems to be considerable variation in the epigynum and internal ducts (if they all belong to one species). Females vary in total length from 6.4 mm (central Mexico) to 8.7 mm (Costa Rica).

Diagnosis. The females are larger and darker than sympatric species (Fig. 598) and the epigynum usually has a heavy transverse bar and narrow septum (Figs. 595, 596). The male can be separated from others by the shape of the bulky paracymbium and by the modifications of the proximal end of the cymbium (Figs. 599, 600).

Natural History, Distribution. Found at 1,000 to 2,300 m altitude in cloud forest from Mexico to western Panama (Map 4). The spider makes a web with the hub about one meter above the ground. Webs on Cerro Poás, Costa Rica, have (unlike many other *Chrysometa*) a full circle of sticky spirals, whereas those of other collecting sites have a vacant sector.

Paratypes. MEXICO *Est. Puebla:* near Xicotepec de Juarez, 1,000 m, 17 June 1983, ♀ (W. Maddison, MCZ). COSTA RICA *Prov. San José:* Pico Blanco above Escazu, 2,000 m, March 1983, ♀ (W. Eberhard, 2263, MCZ). *Cartago:* Cerro de la Muerte, Feb. 1979, July 1980, July 1983, 5♀, ♂ (J. Coddington, MCZ, USNM). *Puntarenas:* Monteverde cloud forest, 1,600 m, 24 July 1978, ♀ (C. L. Craig, Y. Lubin, MCZ). PANAMA *Prov. Chiriquí:* above Boquete, 1,200–1,900 m, 11 Aug. 1983, ♀ (H., L. Levi, MCZ); Cerro Punta nr. Guadelupe, 2,300 m, 25–27 Oct. 1983 (Y. Lubin, MCZ).

Chrysometa uaza new species
Figures 601–606; Map 4

Holotype. Female from Cerro Tinajillas, 3,100 m, Prov. Azuay, Ecuador, 18–21 March 1965 (L. Peña, MCZ). The name is an arbitrary combination of letters.

Description. Female. Carapace orange with dark brown marks (Fig. 606). Labium black. Sternum dark brown with median orange longitudinal band. Legs orange with black patches. Dorsum of abdomen with black patches and silver spots on sides (Fig. 606), sides with black streaks; venter black with line of silver spots on each side. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, their diameter from laterals. Posterior median eyes slightly less than their diameter apart, 1.2 diameters from laterals. Abdomen elongate oval. Total length, 8.6 mm. Carapace, 3.8 mm long, 2.8 mm wide. First femur, 5.8 mm; patella and tibia, 7.4 mm; metatarsus, 6.4 mm; tarsus, 2.0 mm. Second patella and tibia, 5.0 mm; third, 2.5 mm; fourth, 3.8 mm.

Variation. Total length of females varies from 8.6 to 9.5 mm.

Diagnosis. The epigynum is distinguished by a relatively narrow septum and by a transverse bar that is indistinct in outline and is variable (Figs. 603, 604).

Paratype. COLOMBIA *Dpto. Cauca:* path from Pilimbalá to Volcán Puracé, 3,690 m, Puracé Natl. Park, 12–13 Jan. 1983, ♀ (J. Kochalka, MCZ).

Chrysometa lancetilla new species
Figures 607–611; Map 4

Holotype. Female holotype and one female paratype from Lancetilla, near Tela, Dpto. Atlantida, Honduras, July 1929 (A. M. Chickering, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, sternum, legs yellow. First two femora with two rows of black dots on ventral side; tibae, metatarsi, tarsi with distal black ring. Dorsum of abdomen with silver spots; sides with silver spots, black posteriorly above spinnerets (Fig. 611); venter with two patches containing silver spots behind epigynum, gray in between and behind extending to spinnerets. Eyes subequal in size. Anterior median eyes their diameter apart, slightly more than their diameter from laterals; posterior median eyes 0.7 diameters apart, 1.2 diameters from laterals. Abdomen oval. Total length, 5.5 mm. Carapace, 2.5 mm long, 1.9 mm wide. First femur, 3.1 mm; patella and tibia, 3.8 mm; metatarsus, 2.9 mm; tarsus, 1.2 mm. Second patella and tibia, 2.9 mm; third, 1.6 mm; fourth, 2.5 mm.

Diagnosis. The epigynum is distinguished from all others by the notches in the anterior lips of the opening on each side of the septum (Fig. 614).

Chrysometa chipinque new species
Figures 612–617; Map 4

Holotype. Male from 5–10 km E of Rayon, Highway 195, near 17°2′N, 93°0′W, cloud forest edge, Chiapas, Mexico, 6 July 1983 (W. Maddison, R. S. Anderson, 83-097, MCZ). The specific name is a noun in apposition after one of the collecting localities.

Description. Female from Puebla. Carapace, sternum, legs orange; carapace with indistinct gray reticulations. Dorsum of abdomen with silver spots and indistinct gray transverse marks; venter gray with pair of patches containing silver spots behind genital groove. Anterior lateral eyes, posterior median eyes equal to 1.2 diameters of anterior medians; posterior lateral eyes slightly more than diameter of anterior median eyes. Anterior median eyes 0.6 diameters apart, same distance from laterals. Posterior median eyes 0.5 diameters apart, their diameter from laterals. Abdomen subspherical. Total length, 3.1 mm. Carapace, 1.6 mm long, 1.2 mm wide. First femur, 2.1 mm; patella and tibia, 2.5 mm; metatarsus, 1.9 mm; tarsus, 0.8 mm. Second patella and tibia, 1.9 mm; third, 0.9 mm; fourth, 1.5 mm.

Male. Carapace yellow, gray on sides of thorax. Sternum, legs yellow, first femur brown. Dorsum of abdomen with large silver patches; no pigment on venter. Anterior lateral eyes, posterior median eyes equal to diameter of anterior medians; posterior lateral eyes 0.8 diameters of anterior medians. Anterior median eyes their diameter apart, their diameter from laterals; posterior median eyes slightly less than their diameter apart, slightly more than their diameter from laterals. Total length, 2.6 mm. Carapace, 1.5 mm long, 1.1 mm wide. First femur, 2.4 mm; patella and tibia, 2.7 mm; metatarsus, 2.4 mm; tarsus, 0.9 mm. Second patella and tibia, 2.1 mm; third, 1.0 mm; fourth, 1.5 mm.

Variation. Females vary in total length from 3.1 to 4.7 mm, males from 2.6 to 2.9 mm.

Diagnosis. The epigynum can be distinguished from that of *C. palenque* by the convex sides of the septum and by the curved arms of the transverse bar (Fig. 614); in posterior view, as in *C. palenque*, the median plate is tripartite. The male palpus is distinguished by the shape of the paracymbium, having in ventral view a mammal head and a flipper (Fig. 616) and

in lateral view a square with three lobes (Fig. 617).

Natural History, Distribution. Specimens have been collected in a cave, and at various elevations, including cloud forests, from Mexico to Guatemala (Map 4).

Paratypes. MEXICO *Est. Nuevo León:* Chipinque Mesa, S of Monterrey, 100.4°W, 23.0°N, 1,500 m, 2 June 1983, ♂ (W. Maddison, R. S. Anderson, no. 83-034, MCZ). *Veracruz:* Cueva del Ojo de Agua, Tlilpan, nr. Orizaba, 4 March 1973, ♀ (J. Reddell, AMNH). *Puebla:* Villa Juarez, 10 Oct. 1947, ♀, 2♂ (H. M. Wagner, AMNH). *Oaxaca:* 27 km SW of Valle Nacional, 24 June 1983, ♂ (W. Maddison, 83-084, MCZ). GUATEMALA San Pedro Yepocapa, March, April 1945, ♀ (H. Elishwitz, AMNH).

Chrysometa cambara new species
Figures 618–623; Map 4

Holotype. Female holotype and one female paratype from Itaimbézinho, Cambara do Sul, Est. Rio Grande do Sul, Brazil, 5 Jan. 1985, one female, 6 Jan. 1985 (A. Lise, no. 12795, MCN). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellowish with median dusky band; sternum dusky yellowish; legs yellowish with indistinct dusky rings. Dorsum of abdomen with silver spots concentrated into lateral band, posteriorly with pairs of black transverse bars; sides with silver spots, dusky posteriorly; venter black with a longitudinal line on each side of silver spots. Eyes subequal in size. Anterior median eyes 0.8 diameters apart, their diameter from laterals. Posterior median eyes 0.8 diameters apart, 1.2 diameters from laterals. Abdomen narrow, elongate oval. Total length, 5.0 mm. Carapace, 2.4 mm long, 1.8 mm wide. First femur, 4.4 mm; patella and tibia, 5.4 mm; metatarsus, 5.2 mm; tarsus, 1.5 mm. Second patella and tibia, 3.7 mm; third, 1.7 mm; fourth, 2.8 mm.

Male. Carapace orange, head area brown, brown extending to thoracic depression; sternum orange; legs light orange with dark rings. Dorsum of abdomen gray with black spots on shoulders and transverse black bands on posterior half forming median band; venter with black patch on gray, no light lines. Secondary eyes equal to 0.8 diameters of anterior median eyes. Anterior median eyes 0.7 diameters apart, 0.5 diameters from laterals. Posterior median eyes 0.7 diameters apart, their diameter from laterals. Abdomen oval. Total length, 3.8 mm. Carapace 2.0 mm long, 1.6 mm wide. First femur, 3.9 mm; patella and tibia, 4.8 mm; metatarsus, 3.8 mm; tarsus, 1.1 mm. Second patella and tibia, 3.1 mm; third, 1.4 mm; fourth, 2.0 mm.

Note. It is not certain that the males and females belong together.

Variation. Total length of females 5.0 to 6.4 mm.

Diagnosis. The sclerotized dark lobes on each side of the septum of the epigynum (Fig. 620) distinguish this from all other species; in posterior view the lobes form a V (Fig. 621). The paracymbium of the male palpus, wider than long in lateral view (Fig. 623), and with the "upper" and "lower" prongs at right angles in ventral view (Fig. 622), distinguishes males.

Paratypes. BRAZIL *Est. Rio de Janei-*

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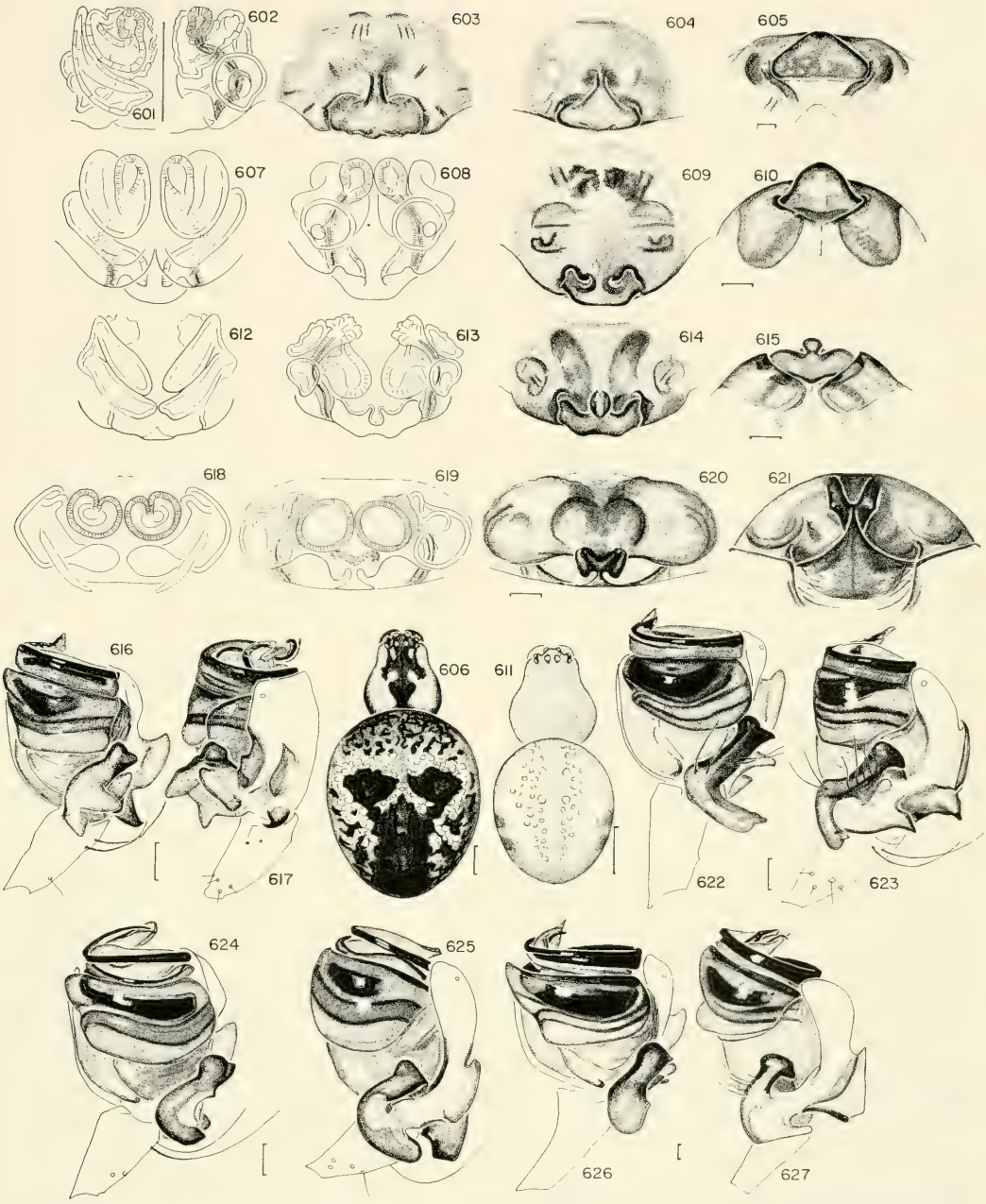
Figures 601–606. *Chrysometa uaza* n. sp. 601–604. Epigynum. 601. Dorsal, cleared. 602. Ventral, cleared. 603, 604. Ventral. 605. Posterior. 606. Female. 601, 604. (Holotype).

Figures 607–611. *C. lancetilla* n. sp. 607–610. Epigynum. 607. Dorsal, cleared. 608. Ventral, cleared. 609. Ventral. 610. Posterior. 611. Female.

Figures 612–617. *C. chipinque* n. sp. 612–615. Epigynum. 612. Dorsal, cleared. 613. Ventral, cleared. 614. Ventral. 615. Posterior. 616, 617. Left male palpus. 616. Ventral. 617. Lateral.



Figures 618–623. *C. cambara* n. sp. 618–621. Epigynum. 618. Dorsal, cleared. 619. Ventral, cleared. 620. Ventral. 621. Posterior. 622, 623. Male palpus. 622. Ventral. 623. Lateral.

Figures 624, 625. *C. ramon* n. sp., male palpus. 624. Ventral. 625. Lateral.

Figures 626, 627. *C. columbicola* Strand, male palpus. 626. Ventral. 627. Lateral.

Scale lines. 0.1 mm, except Figures 606, 611, 1.0 mm.

ro: Teresópolis, 1,800 m, 15 March 1946, ♀, open stone cave, 2,100 m, 15 March 1946, ♀ (both H. Sick, AMNH). *Rio Grande do Sul:* Porto Alegre, 15 Aug. 1976, ♂ (P. A. Buckup, MCN), Itaimbézinho, Cambara do Sul, 5 Jan. 1985, ♀ (A. A. Lise, MCN).

Chrysometa ramon new species
Figures 624, 625; Map 4

Holotype. Male from Estancia Naranjal, 1,000 m, San Ramon, Dept. Junín, Peru, 20–27 July 1965 (P., B. Wygodzinsky, AMNH). The specific name is a noun in apposition after the type locality.

Description. Male. Carapace, sternum orange, margin of thorax and head to thoracic depression darker; labium brown; legs distal end of first tibia gray. Dorsum of abdomen with a few white spots; sides with white pigment spots, posteriorly with indistinct transverse gray marks. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, same distance from laterals. Posterior median eyes 0.5 diameters apart, slightly more than their diameter from laterals. Abdomen narrow oval. Total length, 3.8 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 3.9 mm; patella and tibia, 4.9 mm; metatarsus, 5.2 mm; tarsus, 1.3 mm. Second patella and tibia, 2.9 mm; third, 1.3 mm; fourth, 2.1 mm.

Diagnosis. The palpus of this species differs from others by having two coils of the embolus and its supports above the tegulum (Figs. 624–625), and the "lower" end of the paracymbium is heavier (Fig. 625) than that of *C. columbicola.*

Chrysometa columbicola Strand
Figures 626, 627; Map 4

Chrysometa columbicola Strand, 1915: 103. Male holotype from Popayán, Prov. Cauca, Colombia (SMF), examined. Roewer, 1942: 913. Bonnet, 1956: 1082.

Description. Male. Carapace, legs yellow-brown. Chelicerae dark brown. Dorsum of abdomen with silver spots, except no spots in narrow dorsal longitudinal line, on an anterior cross band, and on shallow humps. Sides, venter with silver spots. Thoracic depression deep. Eyes subequal in size. Anterior medians their diameter apart, slightly more than their diameter from laterals. Posterior median eyes slightly less than their diameter apart, 1.6 from laterals. Legs long. Abdomen oval, widest anteriorly, with indications of dorsal humps. Total length, 7.5 mm. Carapace, 3.5 mm long, 2.8 mm wide. First femur, 9.6 mm; patella and tibia, 12.3 mm; metatarsus, 8.4 mm; tarsus, 5.7 mm. Second patella and tibia, 6.7 mm; third, 3.8 mm; fourth, 5.8 mm.

Diagnosis. The large size and long legs set this specimen apart. The palpus is distinguished by having three coils of the embolus, two behind the tegulum wall, and by the shape of the paracymbium which has a dorsally directed finger on its base (Figs. 626, 627).

Note. Figures 626, 627 are the mirror images of the right palpus.

Chrysometa eugeni new species
Figures 628–634; Map 4

Chrysometa tenuipes:—Simon, 1897: 870 (misidentification, not *C. tenuipes* Keyserling).

Holotype. Female holotype and five females, three male paratypes from St.Vincent Island, Lesser Antilles (BMNH); one female, one male, one immature (MNHN). The species is named after E. Simon.

Description. Female. Carapace, sternum yellow; legs yellow with distal ends of tibiae, metatarsi, and tarsi orange. Dorsum, sides of abdomen with silver spots more than their diameter apart, largest ones on sides; venter with few silver spots. Eyes subequal in size, small. Anterior median eyes their diameter apart, three diameters from laterals. Posterior median eyes 1.7 diameters apart, same distance from laterals. Abdomen oval, slightly pointed anteriorly (Fig. 632). Total length, 4.5 mm. Carapace, 1.9 mm; long, 1.3 mm wide. First femur, 3.0 mm; patella and tibia, 3.5 mm; metatarsus, 3.1 mm; tarsus, 1.1 mm. Second patella and tibia, 2.5 mm; third, 1.3 mm; fourth, 2.1 mm.

Male. Coloration like female. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, 2 diameters from laterals. Posterior median eyes 1.5 diameters apart, same distance from laterals. Abdomen elongate, pointed anteriorly, with slight hump posteriorly. Total length, 3.8 mm. Carapace, 1.8 mm long, 1.4 mm wide. First femur, 3.9 mm; patella and tibia, 4.8 mm; metatarsus, 4.6 mm; tarsus, 1.2 mm. Second patella and tibia, 3.1 mm; third, 1.5 mm; fourth, 2.4 mm.

Diagnosis. The epigynum is separated from that of *C. flavicans* by having shadows of loops anterior of the sculpturing and by having the anterior lips of the depressions overlapping the septum (Fig. 630). The male is distinguished by a unique hook of the distal end of the embolus and its supporting structures (Figs. 633, 634).

Chrysometa flavicans (Caporiacco), new combination
Figures 635–639; Map 4

Pseudometa flavicans Caporiacco, 1947: 24. Female holotype from valley of Demerara River, Guyana (MZUF), examined.
Capichameta flavicans:—Brignoli, 1983: 227.

Description. Female. Carapace light orange-yellow; sternum orange; legs orange-yellow, ringed. Dorsum of abdomen with indistinct gray pattern underlain by silver spots about their diameter apart (Fig. 639), venter gray. Eyes small, subequal in size. Anterior median eyes their diameter apart, 1.5 diameters from laterals. Posterior median eyes their diameter apart, 2 diameters from laterals. Abdomen soft and elongate. Total length, 5.9 mm. Carapace, 2.5 mm long, 2.0 mm wide. First femur, 3.9 mm; patella and tibia, 5.0 mm; metatarsus, 4.2 mm; tarsus, 1.3 mm. Second patella and tibia, 3.2 mm; third, 1.9 mm; fourth, 3.0 mm.

Variation. Total length of females varies from 5.9 to 6.9 mm.

Diagnosis. The epigynum differs from that of *C. eugeni* by having the septum overlap the anterior margins of the depressions and by lacking the paired dark loops anterior of its sculpturing (Fig. 637).

Natural History, Distribution. This is a low altitude forest species found from Guyana to the Amazon area (Map 4).

Records. SURINAM *Brokopondo Prov.:* Browns Berg, 20 Feb. 1982, 2♀ (D. Smith Trail, MCZ). BRAZIL *Est. Amazonas:* Reserva Ducke, Manaus, Aug. 1971, ♀ (M. E. Galiano, MG).

Chrysometa puebla new species
Figures 640–646; Map 4

Holotype. Male holotype and female abdomen from Río Frio, 3,000 m, Puebla, Mexico, 26 April 1942 (C. Bolivar, C. Osorio, D. Pelaez, AMNH).

Description. Female. Abdomen oval (Fig. 644).

Male. Carapace light orange with two paraxial dusky lines extending posteriorly from posterior median eyes and fusing at thoracic depression; sternum black with anteromedian longitudinal orange mark; legs orange with indistinct gray rings. Dorsum of abdomen with scattered silver spots, black and gray coloring similar to female (Fig. 644); venter with two silver lines. Secondary eyes equal to 1.2 diameters of anterior median eyes. Anterior median eyes their diameter apart, same distance from laterals. Posterior median eyes slightly less than their diameter apart, their diameter from laterals. Abdomen oval. Total length, 4.5 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 4.8 mm; patella and tibia, 6.1 mm; metatarsus, 5.3 mm; tarsus, 1.6 mm. Second patella and tibia, 3.8 mm; third, 1.5 mm; fourth, 2.5 mm.

Diagnosis. The epigynum is distinguished by the narrow septum with strongly concave sides, by the distal part of the posterior transverse bar being a dark lobe (Fig. 642) and by the pentagonal median plate in posterior view (Fig. 643). The male has two loops of embolus and supporting structures above the tegulum (Figs. 645, 646) and a paracymbium with an

"upper" pointed knob and a "lower" point (Fig. 646).

Chrysometa tenuipes (Keyserling) Figures 647–651; Map 4

Tetragnatha tenuipes Keyserling, 1863: 147, pl. 7, figs. 12, 13, ♀ [not fig. 14, ♂]. Female lectotype here designated, five female paralectotypes of this species from Santa Fé de Bogota [Bogotá], Colombia, and three female, one juvenile, one male paralectotypes, which are actually *C. bolivia* (BMNH), examined.

Argyroepeira tenuipes:—Keyserling, 1893: 335, pl. 17, fig. 247 [♀ not ♂].

Chrysometa tenuipes:—Roewer, 1942: 914. Bonnet, 1956: 1083. [not Chrysometa tenuipes:—Simon].

Note. A specimen that Keyserling (1863) had illustrated was chosen as lectotype.

Description. Female. Carapace yellow, sides and middle of thorax orange; sternum, legs yellow, distal ends of tibiae red-brown. Dorsum of abdomen with silver patches their diameter apart, absent from midline, from around pedicel, and near spinnerets. Eyes subequal in size. Anterior median eyes their diameter apart, 1.3 diameters from laterals. Posterior median eyes 1.2 diameters apart, same distance from laterals. Abdomen oval, narrow anteriorly, wide and rounded posteriorly (Fig. 651). Total length, 8.3 mm. Carapace, 2.8 mm long, 1.8 mm wide. First femur, 3.4 mm; patella and tibia, 6.4 mm; metatarsus, 6.3 mm; tarsus, 1.9 mm. Second patella and tibia, 4.5 mm; third, 2.3 mm; fourth, 3.5 mm.

Diagnosis. The female is distinguished by the shape of the abdomen (Fig. 651), the long septum of the epigynum, and the paired, curved, diagonal shadows of the connecting ducts anterior of the sculpturing (Fig. 649).

Chrysometa macuchi new species Figures 652–657; Map 4

Holotype. Female from Macuchi, 0°59'S, 79°04'W, Prov. Cotopaxi, Ecuador, March 1943 (H. E. Frizzell, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange with black marks; sternum orange, sides darker; legs ringed orange and black. Dorsum of abdomen with silver spots and black marks (Fig. 656); venter with black marks different from other species (Fig. 657). Anterior lateral eyes equal to 1.3 diameters of anterior medians; posterior median eyes equal to diameter of anterior median eyes, posterior laterals equal to 1.2 diameters of anterior medians. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes slightly less than their diameter apart, slightly more than their diameter from laterals. Abdomen spherical (Fig. 656). Total length, 4.7 mm. Carapace, 1.8 mm long, 1.5 mm wide. First femur, 3.1 mm; patella and tibia, 3.6 mm; metatarsus, 2.3 mm; tarsus, 0.9 mm. Second patella and tibia, 2.5 mm; third, 1.2 mm; fourth, 1.8 mm.

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Figures 628–634. *Chrysometa eugeni* n. sp. 628–631. Epigynum. 628. Dorsal, cleared. 629. Ventral, cleared. 630. Ventral. 631. Posterior. 632. Female. 633, 634. Left male palpus. 633. Ventral. 634. Lateral.

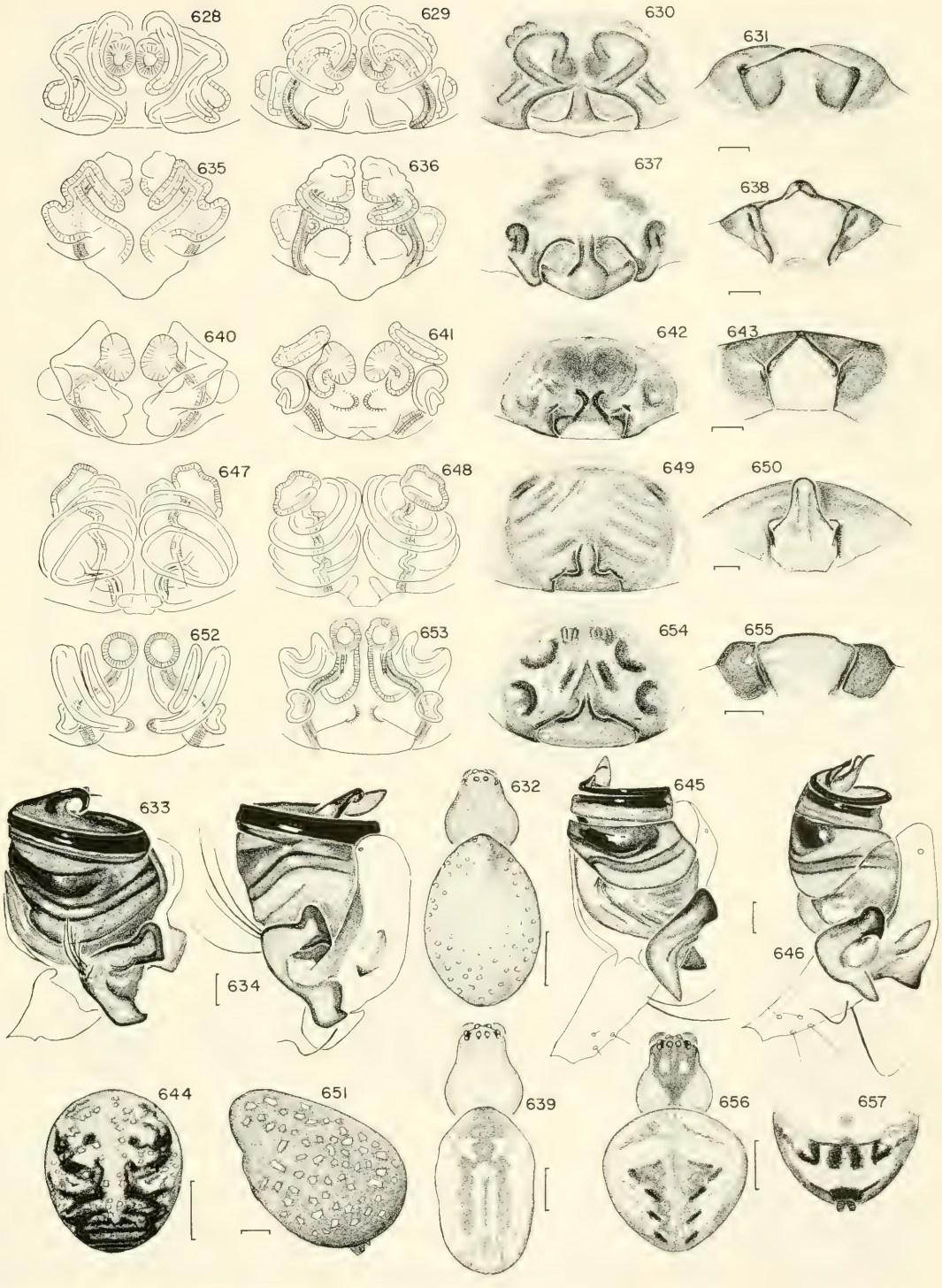
Figures 635–639. *C. flavicans* (Caporiacco). 635–638. Epigynum. 635. Dorsal, cleared. 636. Ventral, cleared. 637, Ventral. 638, Posterior. 639. Female.

Figures 640–646. *C. puebla* n. sp. 640–643. Epigynum. 640. Dorsal, cleared. 641. Ventral, cleared. 642. Ventral. 643. Posterior. 644. Female abdomen, dorsal. 645, 646. Male palpus. 645. Ventral. 646. Lateral.

Figures 647–651. *C. tenuipes* (Keyserling). 647–650. Epigynum. 647. Dorsal, cleared. 648. Ventral, cleared. 649. Ventral. 650. Posterior. 651. Female abdomen, lateral.

Figures 652–657. *C. macuchi* n. sp. 652–655. Epigynum. 652. Dorsal, cleared. 653. Ventral, cleared. 654. Ventral. 655. Posterior. 656. Female. 657. Female abdomen, ventral.

Scale lines. 0.1 mm, except Figures 632, 639, 644, 651, 656, 657, 1.0 mm.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Diagnosis. This species can be distinguished by the ventral markings of the abdomen (Fig. 657), and by the epigynum which has a narrow septum within a triangular depression and paired curved marks anterior of the sculptured area (Fig. 654).

Paratype. PERU *Dpto. Cajamarca:* W of Porcullo [Porculla, 2,145 m, Piura, 05°51'S, 79°31'W], May 1967, ♀ (S. Risco, A. Archer, AMNH).

Chrysometa muerte new species
Figures 658–662; Map 4

Holotype. Female from Cerro de La Muerte, Cartago Prov., Costa Rica, 27 Aug. 1980 (J. Coddington, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow with brown pattern (Fig. 662); sternum brown, lightest in center. Coxae light yellow; legs yellow, ringed. Dorsum of abdomen with black marks and tiny silver spots (Fig. 662); venter with black patch between epigynum and spinnerets, longitudinal line of silver spots along each side. Anterior lateral eyes 1.3 diameters of anterior medians; posterior median eyes 1.3 diameters, posterior laterals 1.2 diameters. Anterior median eyes their diameter apart, same distance from laterals. Posterior median eyes 0.8 diameters apart, slightly more than their diameter from laterals. Abdomen oval. Total length, 4.5 mm. Carapace, 1.9 mm long, 1.3 mm wide. First femur, 3.0 mm; patella and tibia, 3.7 mm; metatarsus, 2.7 mm; tarsus, 1.2 mm. Second patella and tibia, 2.5 mm; third, 1.2 mm; fourth, 1.8 mm.

Diagnosis. This species is smaller than *C. poas* but has a similar epigynum (Fig. 660). The epigynum is distinguished by the paired dark marks anterior of the sculptured area (Fig. 660) and by the relatively simple internal genitalia (Figs. 658, 659).

Record. COLOMBIA *Dpto. Valle:* Río Tulva near Mateguadua, 1,100 m, Aug. 1977, ♀ (determination uncertain) (W. Eberhard, MCZ).

Chrysometa palenque new species
Figures 663–666; Map 4

Holotype. Female from Palenque ruins, Chiapas, Mexico, 28 May 1980 (J. Coddington, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow with contrasting black marks; chelicerae orange with gray; sternum gray on orange; legs yellow, ringed gray. Dorsum of abdomen with few white pigment spots except on sides and in patch above spinnerets; venter black with white band on each side narrowing posteriorly. Eyes subequal in size. Anterior median eyes 0.7 diameters apart, same distance from laterals. Posterior median eyes 0.7 diameters apart, 1.2 diameters from laterals. Abdomen oval. Total length, 6.5 mm. Carapace, 2.8 mm long, 2.1 mm wide. First femur, 3.5 mm; patella and tibia, 4.2 mm; metatarsus, 3.2 mm; tarsus, 1.3 mm. Second patella and tibia, 3.1 mm; third, 1.7 mm; fourth, 2.5 mm.

Male. The palpus of a male found after completion of the revision was similar to that of *C. universitaria.*

Note. Abdomen is in poor condition.

Diagnosis. The epigynum of this species is distinguished by wide, bulging ends of the transverse bar, the anterior end of the bulge being about in line with the anterior end of the septum (Fig. 665). In posterior view the median plate appears tripartite (Fig. 666).

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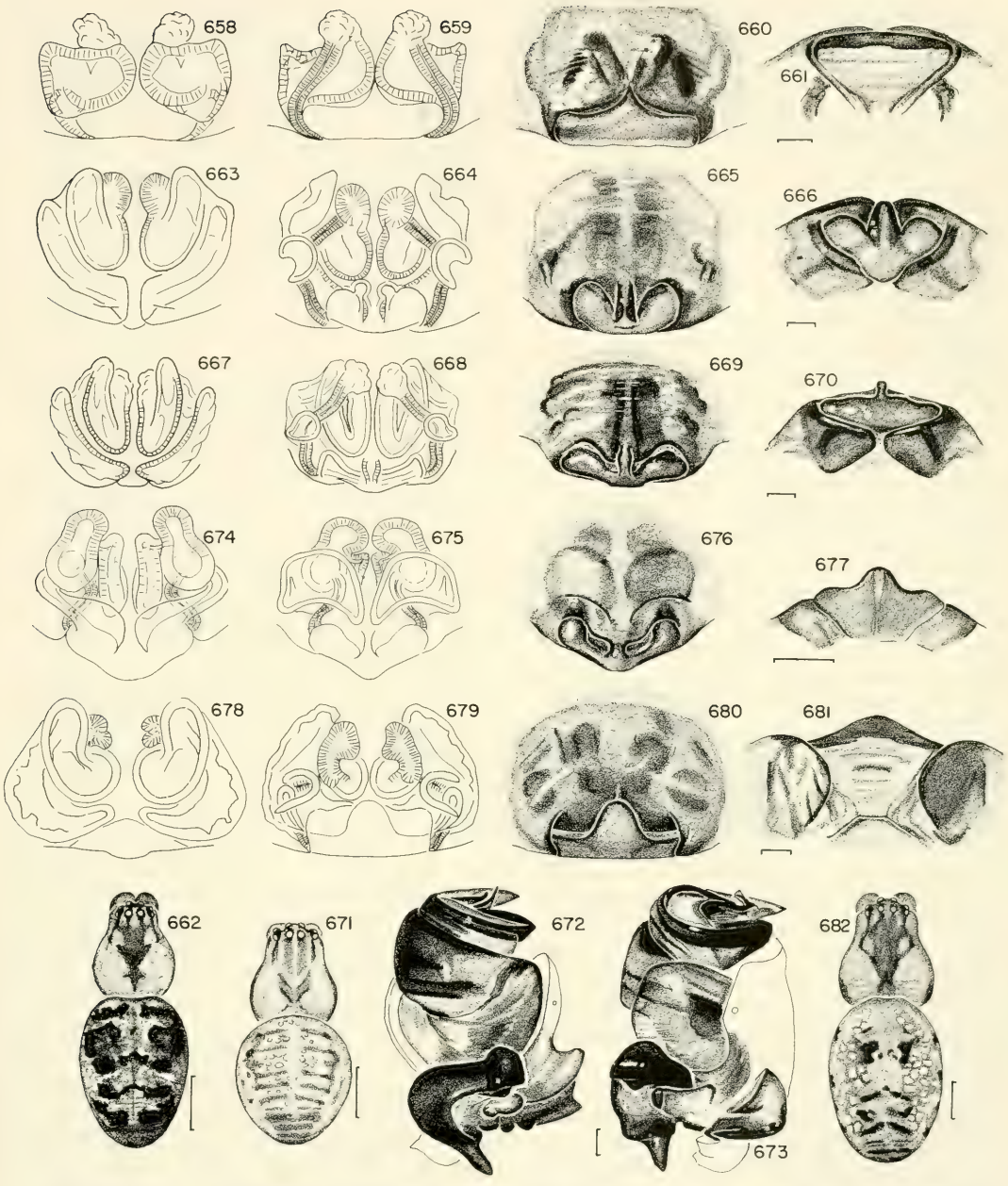
Figures 658–662. *Chrysometa muerte* n. sp. 658–661. Epigynum. 658. Dorsal, cleared. 659. Ventral, cleared. 660. Ventral. 661. Posterior. 662. Female.

Figures 663–666. *C. palenque* n. sp., epigynum. 663. Dorsal, cleared. 664. Ventral, cleared. 665. Ventral. 666. Posterior.



Figures 667–673. *C. universitaria* n. sp. 667–670. Epigynum. 671. Female. 672, 673. Left male palpus. 672. Ventral. 673. Lateral.

Figures 674–677. *C. otavalo* n. sp., epigynum. 674. Dorsal, cleared. 675. Ventral, cleared. 676. Ventral. 677. Posterior.

Figures 678–682. *C. incachaca* n. sp. 678–681. Epigynum. 678. Dorsal, cleared. 679. Ventral, cleared. 680. Ventral. 681. Posterior. 682. Female.

Scale lines. 0.1 mm, except Figures 662, 671, 682, 1.0 mm.

Paratypes. HONDURAS *Dpto. Atlantida*: Lancetilla, July 1929, 5♀, ♂ (A. M. Chickering, AMNH, MCZ, USNM).

Chrysometa universitaria new species
Figures 667–673; Map 4

Holotype. Female from Ciudad Universitaria, San José, Costa Rica, 10 Jan. 1979 (J. Coddington, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace yellow with gray streaks. Legs yellow, ringed. Dorsum of abdomen with silver spots and transverse bars (Fig. 671). Anterior lateral eyes, posterior median eyes 1.3 diameters of anterior medians; posterior lateral eyes equal to diameter of anterior medians. Anterior median eyes 0.8 diameters apart, their diameter from laterals. Posterior median eyes 0.5 diameters apart, their diameters from laterals. Abdomen oval. Total length, 4.5 mm. Carapace, 2.0 mm long, 1.6 mm wide. First femur, 2.6 mm; patella and tibia, 3.1 mm; metatarsus, 2.4 mm; tarsus, 1.1 mm. Second patella and tibia, 2.4 mm; third, 1.3 mm; fourth, 1.9 mm.

Male from Volcán, Panama. Coloration like female. Eyes subequal in size. Anterior median eyes their diameter apart, slightly less than their diameter from laterals. Posterior median eyes 0.5 diameters apart, their diameter from laterals. Abdomen oval. Total length, 4.2 mm. Carapace, 2.1 mm long, 1.8 mm wide. First femur, 3.1 mm; patella and tibia, 3.8 mm; metatarsus, 3.1 mm; tarsus, 1.1 mm. Second patella and tibia, 3.0 mm; third, 1.3 mm; fourth, 1.9 mm.

Variation. Females vary in total length from 3.8 to 5.2 mm.

Diagnosis. The epigynum of this species is distinguished from *C. chipinique* and *C. palenque* by a wider transverse bar and smaller septum and from *C. chipinique* by the swellings of the bar's arm and by the anterior longitudinal parallel dark marks (Fig. 669). The palpus of the male has a heavily sclerotized paracymbium curved in ventral view (Fig. 672) with a "lower" thumb in lateral view (Fig. 673).

Natural History, Distribution. Found at 1,300 to 1,500 m in Costa Rica and western Panama (Map 4).

Paratypes. COSTA RICA *Prov. Heredia:* NE of San Rafael, 1,400 m, June 1980, 4♀ (W. Eberhard, MCZ). *San José:* San José, 30 Sept. 1980, ♀ (R. W. Work, W. Eberhard, MCZ); Ciudad Universitaria, 10 Jan. 1979, ♀ (J. Coddington, MCZ); San Antonio de Escazú, 1,300 m, 1981, ♀ (W. Eberhard, MCZ). *Puntarenas:* Monteverde, Campbell's Woods, 1,500 m, 8 Feb. 1979, 2♀ (J. Coddington, MCZ); Monteverde, Biological Reserve, 8 Feb. 1979, ♀ (J. Coddington, MCZ). PANAMA *Prov. Chiriquí:* Boquete, Aug. 1954, ♀ (A. Chickering, MCZ); Volcán, 20 Feb. 1936, 7♀, 2♂, 2 Mar. 1936, ♀, 2♂, 26 Feb. 1936, ♀ (W. J. Gertsch, AMNH); near Río Sereno, 10 Aug. 1983, ♀ (L. N. Sorkin, AMNH).

Chyrysometa otavalo new species
Figures 674–677; Map 4

Holotype. Female from Otavalo, Atuela, 2,200 m ? Prov. Pichincha, Ecuador, 8–9 Sept. 1977 (L. Peña, AMNH). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace orange, black between anterior median eyes; sternum orange-brown; legs orange, distal articles darker, without rings. Dorsum of abdomen with silver spots, except above heart and some posteriorly pointing branches; sides without spots; venter with rectangular gray patch, with pair of silver spots anterior of spinnerets, and black mark on each side of spinnerets. Anterior lateral eyes, posterior median eyes equal to 1.3 diameters of anterior medians; posterior lateral eyes equal to 1.2 diameters of anterior medians. Anterior median eyes slightly less than their diameter apart, slightly more than their diameter from laterals. Posterior median eyes slightly less than their diameter apart, 1.3 diameters from laterals. Abdomen oval, sides almost parallel, anterior and posterior equally

rounded. Total length, 3.0 mm. Carapace, 1.1 mm long, 1.0 mm wide. First femur, 1.7 mm; patella and tibia, 2.0 mm; metatarsus, 1.7 mm; tarsus, 0.7 mm. Second patella and tibia, 1.6 mm; third, 0.8 mm; fourth, 1.1 mm.

Diagnosis. The epigynum of this species is distinguished by the rims of the septum continuing anteriorly and diagonally and surrounding the ends of the transverse bar (Fig. 676). There is a pair of round dark patches anterior of the lateral ends of the bar (Fig. 676).

Chrysometa incachaca new species
Figures 678–682; Map 4

Holotype. Female from Incachaca, 2,100 m, Dpto. Cochabamba, Bolivia, 30 Aug. 1956 (L. Peña, IRSNB). The species name is a noun in apposition after the type locality.

Description. Female. Carapace light orange with brown pattern; sternum light orange; legs light orange, indistinctly ringed. Dorsum of abdomen with black marks on shoulders, broken chevrons posteriorly, and large silver spots on sides (Fig. 682); sides with scattered small silver spots and black marks; venter with two light longitudinal lines of small silver spots and a pair of dusky streaks anterior of spinnerets. Anterior lateral eyes equal to 1.4 diameters of anterior medians; posterior median eyes equal to 1.3 diameters; posterior laterals equal to diameter of anterior median eyes. Anterior median eyes slightly more than their diameter apart, same distance from laterals. Posterior median eyes 0.8 diameters apart, 1.3 diameters from laterals. Abdomen elongate oval. Total length, 6.2 mm. Carapace, 2.7 mm long, 2.0 mm wide. First femur, 4.5 mm; patella and tibia, 5.7 mm; metatarsus, 5.2 mm; tarsus, 1.9 mm. Second patella and tibia, 3.9 mm; third, 1.9 mm; fourth, 2.8 mm.

Diagnosis. The epigynum of this species is distinguished by a swollen septum, a median projection of the transverse bar (Fig. 680).

Chrysometa calima new species
Figures 683–690; Map 4

Holotype. Female from Lago Calima, 1,400 m, Dpto. Valle, Colombia, Jan. 1979 (W. Eberhard, no. 1824, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, sternum and legs yellow. Dorsum of abdomen with silver spots; venter with silver spots only on sides. Eyes small, subequal in size. Anterior median eyes 1.5 diameters apart, more than twice their diameter from laterals. Posterior median eyes less than 2 diameters apart, more than twice their diameter from laterals. Clypeus equal to 1.5 diameters of anterior median eyes. Abdomen oval with a slight median anterior hump (Fig. 688). Total length, 5.4 mm. Carapace, 2.1 mm long. 1.5 mm wide. First femur, 3.0 mm; patella and tibia, 3.6 mm; metatarsus, 3.1; tarsus, 1.1 mm. Second patella and tibia, 2.5 mm; third, 1.3 mm; fourth, 2.1 mm.

Male. Coloration lighter than female, with some black spots on dorsum of abdomen. Eyes like female. Total length, 3.8 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 4.0 mm; patella and tibia, 4.9 mm; metatarsus, 5.1 mm; tarsus, 1.3 mm. Second patella and tibia, 2.9 mm; third, 1.5 mm; fourth, 2.3 mm.

Variation. Females vary in total length from 5.2 to 6.2 mm, males from 3.8 to 5.2 mm.

Diagnosis. The epigynum of this species has septum and bar surrounded by a semicircular lip; the openings are diagonal notches on each side (Fig. 685). In ventral view (Fig. 689) the paracymbium resembles that of *C. universitaria*, in lateral view the "lower" prong is curved at a right angle (Fig. 690).

Natural History, Distribution. Found 1,000 to 1,500 m, in Colombia (Map 4).

Paratypes. COLOMBIA *Dpto. Magdalena*, Sierra Nevada de Santa Marta: Valle Leonor, Serra Nueva Granada, 1,300 m, 12 April 1975, ♂ (J. Kochalka, MCZ);

Serra Nueva Granada, 1,500 m, 28 April 1975, 2♀ (J. Kochalka, MCZ); San Pedro, 1,100–1,200 m, 3 April 1975, 19 May 1975, 2♀ (J. Kochalka, IBNA). *Valle:* Cali, 1,000 m, 1973–1974, ♂ (W. Eberhard, MCZ); Lago Calima, 1,400 m, Jan. 1979, ♀, 4♂ (W. Eberhard, no. 1824, 1850, MCZ).

Chrysometa opulenta (Keyserling) Figures 691–698; Map 4

Meta opulenta Keyserling, 1880: 558, pl. 16, fig. 9, ♀, ♂. Male lectotype here designated, one female paralectotype from Paltaypampa [1,860 m, Dpto. Junín, Prov. Tarma], Peru; two female paralectotypes from Amable María [3,800 m, Dpto. Junín, Prov. Tarma], Peru, (PAN), examined.

Argyoepeira opulenta:—Keyserling, 1893: 346, pl. 18, fig. 245, ♀, ♂.

Chrysometa opulenta:—Roewer, 1942: 913. Bonnet, 1956: 1083.

Description. Female from Amable María. Carapae, sternum, legs orange-yellow. Dorsum of abdomen evenly covered with large silver spots, about their diameter apart; venter with fewer spots. Posterior median eyes slightly smaller than others. Anterior median eyes 1.3 diameters apart, slightly less than two diameters from laterals. Posterior median eyes slightly more than their diameter apart, 1.6 diameters from laterals. Abdomen oval with slight anteromedian hump (Figs. 695, 696). Total length, 5.0 mm. Carapace, 1.9 mm long, 1.4 mm wide. First femur, 3.2 mm; patella and tibia, 3.7 mm; metatarsus, 3.4 mm; tarsus, 1.0 mm. Second patella and tibia, 2.4 mm; third, 1.3 mm; fourth, 2.2 mm.

Male from Paltaypampa. Coloration and structure like female. Chelicerae with hump below clypeus. Total length, 3.8 mm. Carapace, 2.0 mm long, 1.7 mm wide. First femur, 4.0 mm; patella and tibia, 4.8 mm; metatarsus, 4.9 mm; tarsus, 1.1 mm. Second patella and tibia, 2.9 mm; third, 1.4 mm; fourth, 2.3 mm.

Variation. Females vary in total length from 5.0 to 7.0 mm.

Diagnosis. The septum and transverse bar of the epigynum form a triangular, posteriorly directed swelling with a pair of depressions (Fig. 693). The paracymbium of the male palpus is similar but smaller than that of *C. universitaria* and *C. calima* but differs in lateral view by a slightly curved "lower" prong (Figs. 697, 698).

Natural History, Distribution. Low elevations to 3,800 m, Peru, Brazil (Map 4).

Records. PERU *Dpto. Huánuco:* Cucharas, Huallaga Valley, Feb.–April, 5♀, imm. (F. Woytkowski, EPC); Tingo María, numerous specimens (AMNH, CAS, MCZ). BRAZIL *Est. Goias:* Faz. Cachveirinha, Jataí, Oct. 1962, ♀ (MZSP).

Chrysometa tungurahua new species Figures 699–702; Map 4

Holotype. Female from Baños, Prov. Tungurahua, Ecuador, 11 Feb. 1955 (E. I. Schlinger, E. S. Ross, CAS). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, sternum, legs orange-yellow. Dorsum of abdomen with scattered white pigment spots;

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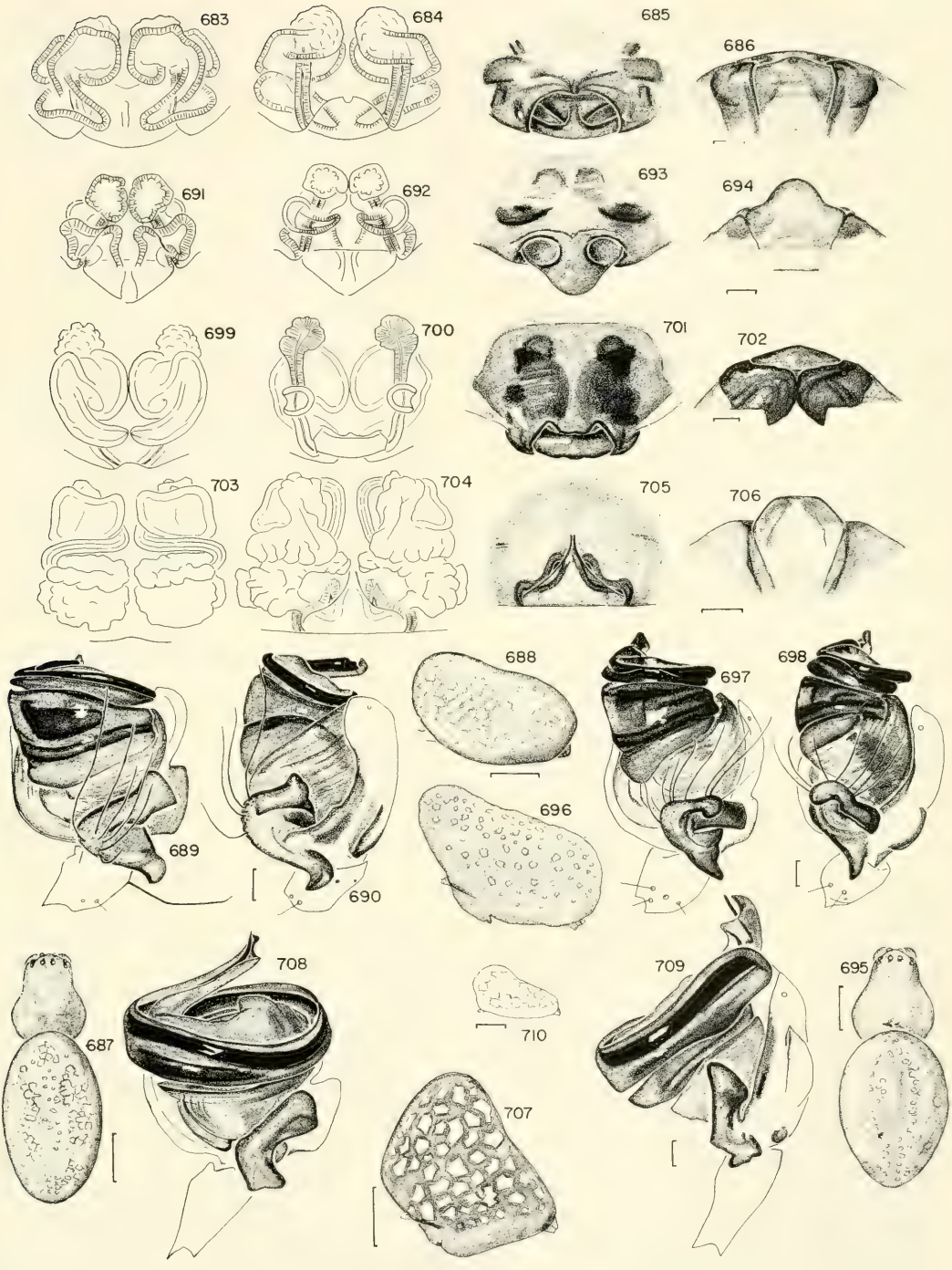
Figures 683–690. *Chrysometa calima* n. sp. 683–686. Epigynum. 683. Dorsal, cleared. 684. Ventral, cleared. 685. Ventral. 686. Posterior. 687. Female. 688. Female abdomen, lateral. 689, 690. Left male palpus. 689. Ventral. 690. Lateral.

Figures 691–698. *C. opulenta* (Keyserling). 691–694. Epigynum. 691. Dorsal, cleared. 692. Ventral, cleared. 693. Ventral. 694. Posterior. 695. Female. 696. Female abdomen, lateral. 697, 698. Male palpus. 697. Ventral. 698. Lateral.

Figures 699–702. *C. tungurahua* n. sp., epigynum. 699. Dorsal, cleared. 700. Ventral, cleared. 701. Ventral. 702. Posterior.

Figures 703–710. *C. bolivia* n. sp. 703–706. Epigynum. 703. Dorsal, cleared. 704. Ventral, cleared. 705. Ventral. 706. Posterior. 707. Female abdomen, lateral. 708, 709. Male palpus. 708. Ventral. 709. Lateral. 710. Male abdomen, lateral.

Scale lines. 0.1 mm, except Figures 687, 688, 695, 696, 707, 710, 1.0 mm.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venter without black band, with bare patch containing silver spots on each side. Anterior lateral eyes, posterior median eyes equal to 1.3 diameters of anterior medians; posterior lateral eyes equal to 1.2 diameters of anterior median eyes. Anterior median eyes their diameter apart, 0.5 diameters from laterals. Posterior median eyes 0.6 diameters apart, their diameter from laterals. Abdomen subspherical. Total length, 4.2 mm. Carapace, 1.8 mm long, 1.4 mm wide. First femur, 2.3 mm; patella and tibia, 2.7 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 2.1 mm; third, 1.1 mm; fourth, 1.6 mm.

Diagnosis. The epigynum of this species is distinguished by lacking a distinct septum, but having a transverse bar touched in the middle by a median lobe (Fig. 701).

Chrysometa bolivia new species
Figures 703–710; Map 4

Holotype. Female from Rurrenabaque, Dpto. El Beni, Bolivia, Oct.–Nov. 1956 (L. Peña, IRSNB). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, sternum yellowish; legs yellowish, black at distal ends of first tibiae, tarsi and metatarsi. Dorsum of abdomen with large silver patches, absent from venter (Fig. 707); venter with black marks on each side of spinnerets. Anterior lateral eyes, posterior median eyes equal to 1.2 diameters of anterior medians; posterior lateral eyes equal to diameter of anterior median eyes. Anterior median eyes slightly less than their diameter apart, 0.6 diameters from laterals. Posterior median eyes their diameter apart, same distance from laterals. Abdomen as high as long (Fig. 707) with two indistinct anterior humps and pointed posterior. Total length, 4.5 mm. Carapace, 1.8 mm long, 1.4 mm wide. First femur, 3.9 mm; patella and tibia, 4.8 mm; metatarsus, 4.4 mm; tarsus, 1.5 mm. Second patella and tibia, 2.9 mm; third, 1.5 mm; fourth, 2.4 mm.

Male from Bogotá, Colombia. Coloration like female, but silver spots on abdomen much closer together, almost touching. Eyes subequal in size. Anterior median eyes 0.7 diameters apart, 0.7 diameters from laterals. Posterior median eyes their diameter apart, same distance from laterals. Total length, 4.3 mm. Carapace, 1.9 mm long, 1.5 mm wide. First femur, 6.2 mm; patella and tibia, 7.8 mm; metatarsus, 8.6 mm; tarsus 1.6 mm. Second patella and tibia, 4.4 mm; third, 1.9 mm; fourth, 3.0 mm.

Note. The only collection other than the type were three female, one male paralectotypes of *Tetragnatha tenuipes* Keyserling from Bogotá, Colombia, perhaps an erroneous locality (BMNH).

Diagnosis. The epigynum has a triangular septum and transverse bar similar to *C. distincta* but is distinguished from *C. distincta* and *C. tenuipes* by the wavy diagonal lip of the openings on each side (Fig. 705). The male differs from all others by the long conductor and supporting structures and the minute tegulum (Figs. 708, 709).

Chrysometa alajuela new species
Figures 711–717; Map 4

Holotype. Female from Peñas Blancas, headwaters of Río Peñas Blancas, Prov. Alajuela, Costa Rica, 13 Aug. 1980 (J. Coddington, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, legs yellow; legs black on distal ends of tibiae. Dorsum of abdomen with gray marks and scattering of silver spots (Fig. 715); venter with pair of patches side by side behind epigynum, containing small silver spots. Lateral eyes equal to diameter of anterior median eyes; posterior medians 1.2 diameters of anterior median eyes. Anterior median eyes 0.8 diameters apart, 0.8 diameters from laterals; posterior median eyes 0.6 diameters apart, their diameter from laterals. Abdomen oval (Fig. 715). Total length, 5.0 mm. Carapace, 2.3 mm long, 1.8 mm wide. First femur, 2.7

mm; patella and tibia, 3.4 mm; metatarsus, 2.6 mm; tarsus, 1.2 mm. Second patella and tibia, 2.5 mm; third, 1.3 mm; fourth, 2.0 mm.

Male from Volcán, Panama. Coloration lighter than that of female (specimen recently molted). Anterior lateral eyes, posterior median eyes equal to 1.5 diameters of anterior medians; posterior lateral eyes equal to diameter of anterior median eyes. Anterior median eyes slightly more than their diameter apart, same distance from laterals. Posterior median eyes 0.6 diameters apart, 1.5 diameters from laterals. Abdomen oval. Total length, 3.5 mm. Carapace, 1.9 mm long, 1.6 mm wide. First femur, 2.9 mm; patella and tibia, 3.5 mm; metatarsus, 3.0 mm; tarsus, 1.1 mm. Second patella and tibia, 2.5 mm; third, 1.1 mm; fourth, 1.6 mm.

Variation. Other females were 4.2 mm total length.

Note. A male was collected with females.

Diagnosis. The epigynum, smooth in ventral view and extending posteriorly (Fig. 713), and the septum and transverse bar, visible only in posterior view (Fig. 714), distinguish *C. alajuela* from others. The shape of the large paracymbium of the male palpus (Figs. 716, 717) distinguishes the male.

Natural History, Distribution. Found at intermediate altitudes Costa Rica to southern Colombia (Map 4).

Paratypes. COSTA RICA *Prov. Cartago:* Turrialba, May 1944, ♀ (F. Schroeder, AMNH). PANAMA *Prov. Chiriquí:* Volcán, 2 March 1936, 2♀, ♂ (W. J. Gertsch, AMNH). COLOMBIA *Dpto. Valle*: Cent. Hid. del Río Anchicayá, 400 m, 1977, ♀ (W. Eberhard, MCZ).

Chrysometa heredia new species
Figures 718–724; Map 4

Holotype. Male holotype and one female paratype from Finca La Selva, near Puerto Viejo, Heredia Prov., Costa Rica, December 1980 (W. Eberhard, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, legs, sternum orange-yellow. Legs black on distal end of tibiae. Abdomen with silver spots, more than their diameter apart; venter without spots except indication of two lines of silver spots. Anterior lateral eyes equal to diameter of anterior medians; posterior median eyes equal to anterior medians; posterior lateral eyes 0.8 diameters of anterior median eyes. Anterior median eyes slightly less than their diameter apart, 0.7 diameters from laterals. Posterior median eyes slightly less than their diameter apart, slightly more than their diameter from laterals. Abdomen subspherical. Total length, 3.6 mm. Carapace, 1.9 mm long, 1.3 mm wide. First femur, 2.2 mm; patella and tibia, 2.6 mm; metatarsus, 2.1 mm; tarsus, 1.0 mm. Second patella and tibia, 2.0 mm; third, 0.9 mm; fourth, 1.7 mm.

Male. Color like female. Eyes subequal in size, except posterior laterals, 0.8 diameters of anterior medians. Anterior median eyes 0.8 diameters apart, 0.7 from laterals. Posterior median eyes 0.8 diameters apart, their diameter from laterals. Total length, 4.1 mm. Carapace, 2.2 mm long, 1.6 mm wide. First femur, 3.2 mm; patella and tibia, 3.9 mm; metatarsus, 3.2 mm; tarsus, 1.1 mm. Second patella and tibia, 2.9 mm; third, 1.3 mm; fourth, 1.9 mm.

Note. Chrysometa heredia has shorter legs than the sympatric *C. flava.*

Diagnosis. The epigynum is distinguished by the septum forming a T within a frame and being broken before meeting the transverse bar. The bar forms a posterior lip (Figs. 720–722). The male palpus has the embolus moved laterally on the tegulum (Fig. 723, 724), and the paracymbium is heavily sclerotized and almost round in lateral view. The palpus resembles that of *C. alajuela* except for having a thicker embolus and more compact paracymbium (Figs. 723, 724).

Paratypes. Ten collections from type locality, 8♀, 3♂ (J. Coddington, W. Eberhard, no. TL 33-5, TL 53-5, distributed: MCZ, AMNH, BMNH, USNM, SMF).

Chrysometa jordao new species
Figures 725–728; Map 4

Holotype. Female from Campos do Jordão, Est. São Paulo, Brazil, 3 Jan. 1948 (F. Lane, MZSP). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange, head brown between lateral eyes and thoracic depression, enclosing two pairs of lighter orange areas; rim of thorax brown. Labium, endites, sternum dark brown; legs indistinctly ringed brown on orange. Dorsum of abdomen with tiny white spots posteriorly, scattered black spots anteriorly, transverse black marks and spots posteriorly; sides with reticulated gray marks; venter with rectangular black mark limited on each side by light longitudinal band of silver spots. Eyes subequal in size. Anterior median eyes slightly less than their diameter apart, same distance from laterals. Posterior median eyes 0.7 diameters apart, 1.2 diameters from laterals. Abdomen oval, wider anteriorly than posteriorly. Total length, 7.7 mm. Carapace, 3.2 mm long, 2.5 mm wide. First femur, 5.1 mm; patella and tibia, 6.5 mm; metatarsus, 5.6 mm; tarsus, 1.5 mm. Second patella and tibia, 4.7 mm; third, 2.3 mm; fourth, 3.4 mm.

Variation. A second specimen is 6.5 mm total length.

Diagnosis. The epigynum is distinguished by a pair of deep depressions separated by a very narrow septum and a transverse bar that forms a posterior lip of the depression (Fig. 727).

Paratypes. BRAZIL *Est. São Paulo:* Campos do Jordão, March 1945, ♀ (P. Wygodzinsky, MZSP).

Chrysometa churitepui new species
Figures 729, 730; Map 4

Holotype. Male from Churitepui, 1,000 m [Churi-Tepuí], Est. Bolívar, Venezuela, Feb 1935 (AMNH). The specific name is a noun in apposition after the type locality.

Description. Male. Carapace orange, head darkest; sternum orange; legs orange, indistinctly ringed. Dorsum of abdomen with longitudinal band, wider anteriorly than posteriorly, of black shoulder patches and black transverse bars, with silver spots along its sides and behind shoulder patches; sides dusky with a silver stripe; venter dusky on orange, with a round silver patch on each side closer to genital groove than to spinnerets. Anterior lateral eyes, posterior median eyes equal to 0.7 diameters of anterior medians; posterior lateral eyes equal to 0.6 diameters of anterior median eyes. Anterior median eyes their diameter apart, 0.6 diameters from laterals. Posterior median eyes 0.7 diameters apart, 1.5 diameters from laterals. Abdomen oval. Total length, 5.4 mm. Carapace, 2.9 mm long, 2.5 mm wide. First femur, 5.8 mm; patella and tibia, 7.4 mm; metatarsus, 7.5 mm; tarsus, 2.0 mm. Second patella and tibia, 4.3 mm; third, 1.8 mm; fourth, 2.9 mm.

Diagnosis. The palpus differs from that of *C. heredia* and *C. alajuela* by having the paracymbium in lateral view project ventrally and having the proximal end of the cymbium more dissected (Figs. 729, 730).

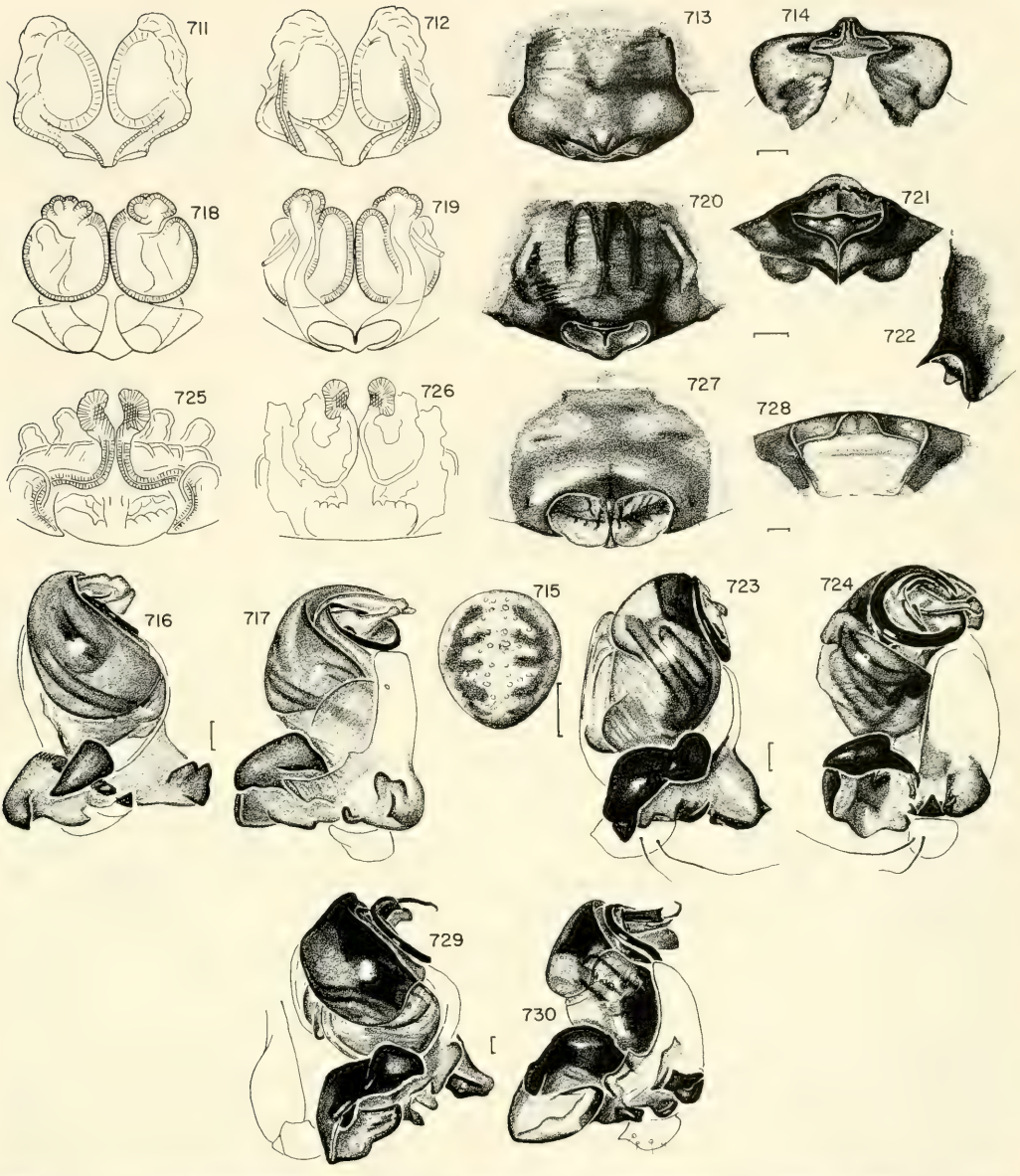
Homalometa Simon

Homalometa Simon, 1897: 872. Type species *H. nigritarsis* Simon by monotypy.

Diagnosis. Homalometa differs from *Chrysometa* and other metines by a male palpus that has a modified, lobed and narrow cymbium and lacks a paracymbium (Figs. 735–739), and by the palpal tibia having a projection (Figs. 735–737).

Females differ by having an epigynum with a transverse swelling (Figs. 731, 747). The chelicerae of *Homalometa* have only two or three teeth on the posterior margin, whereas *Chrysometa* has four.

Description. Carapace, sternum, legs brownish-yellow. Abdomen covered by



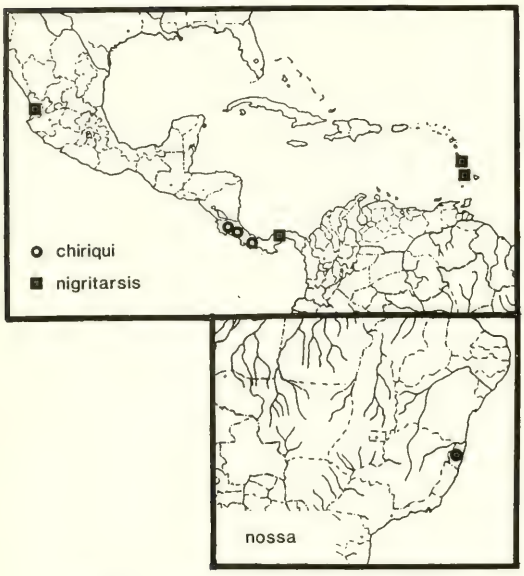
Figures 711–717. *Chrysometa alajuela* n. sp. 711–715. Epigynum. 711. Dorsal, cleared. 712. Ventral, cleared. 713. Ventral. 714. Posterior. 715. Female abdomen, dorsal. 716, 717. Left male palpus. 716. Ventral. 717. Lateral.

Figures 718–724. *C. heredia* n. sp. 718–722. Epigynum. 718. Dorsal, cleared. 719. Ventral, cleared. 720. Ventral. 721. Posterior. 722. Lateral. 723, 724. Male palpus. 723. Ventral. 724. Lateral.

Figures 725–728. *C. jordao* n. sp., epigynum. 725. Dorsal, cleared. 726. Ventral, cleared. 727. Ventral. 728. Posterior.

Figures 729, 730. *C. churitepui* n. sp., male palpus. 729. Ventral. 730. Lateral.

Scale lines. 0.1 mm, except Figure 715, 1.0 mm.



Map 5. Distribution of *Homalometa* species.

white pigment spots except around pedicel, epigynum and spinnerets (Fig. 734).

The carapace is narrow in front, the thoracic depression indistinct. The eyes are subequal in size, the anterior eyes slightly closer to the laterals than to each other, the posterior eyes equally spaced. The lateral eyes on each side touch. The height of the clypeus equals one to two diameters of the anterior median eyes.

The chelicerae have three teeth on the anterior margin, some denticles proximally, two or three on the posterior. The male chelicerae are narrower and slightly longer than those of the female. The first leg is longest, the second slightly longer than the fourth, the third shortest. The abdomen is subspherical.

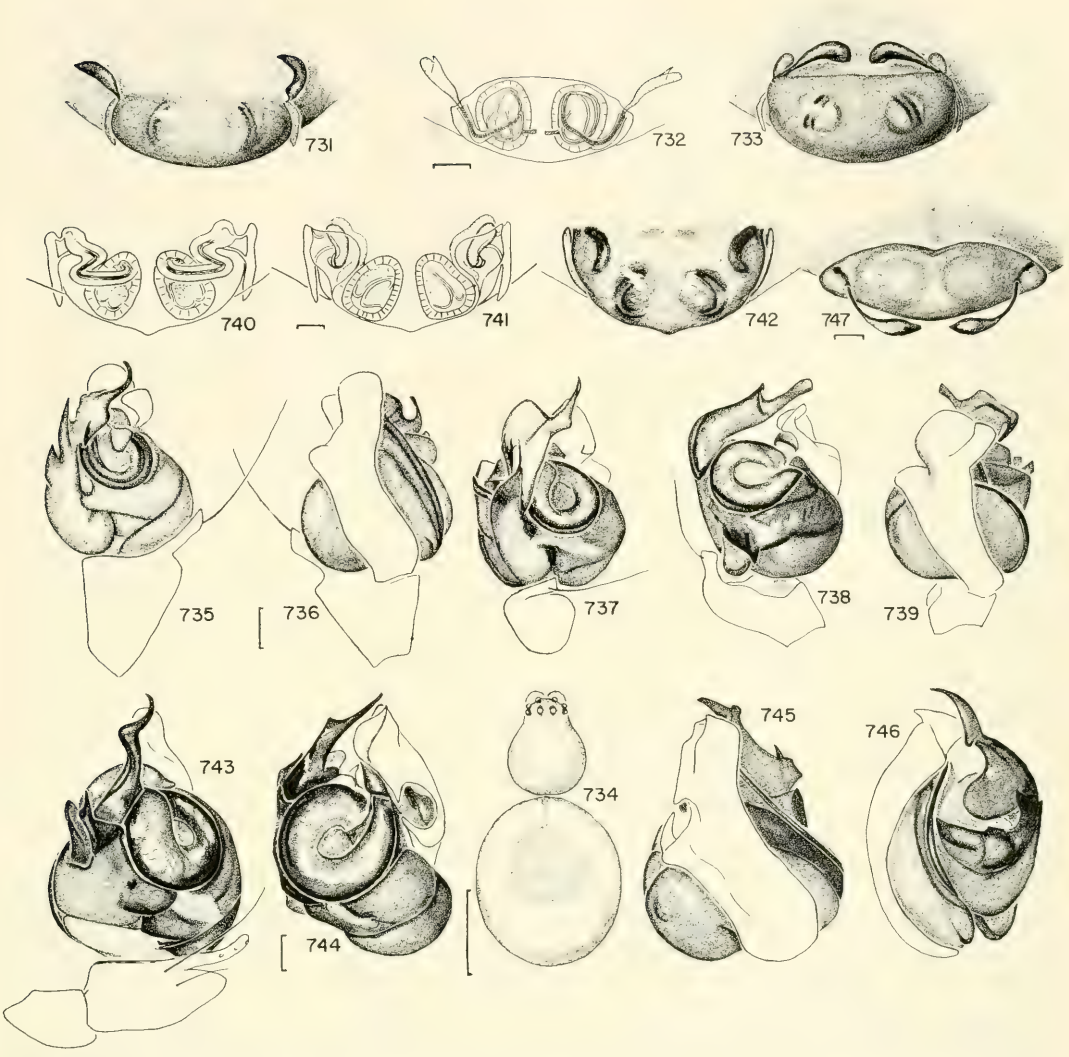
Genitalia. The female epigynum has a transverse swelling with an opening on each side (Figs. 731, 732). There is one pair of seminal receptacles with fertilization ducts that originate medially (Fig. 732). Out of each opening hangs a sclerotized oval balloon-shaped structure, probably a sclerite, left by the male's palpus. If cleared, these structures continue as a double duct and coil inside the seminal receptacles. Inside the seminal receptacles the two parts of the duct appear separated (Figs. 732, 740, 741). In the epigynum of *H. chiriqui*, these probable male structures are hidden in lateral pockets (Figs. 741, 742). Also on the sides hang whitish tubes (Figs. 731, 733 747) that probably come from the male as well. Are they spermatophores?

The narrow cymbium has lobes (Figs. 736, 745), but no paracymbium. The apical transverse projection (Figs. 738, 744) of the palpus appears to be the conductor, and the embolus seems wrapped in the terminal apophysis. The palpal tibia has a projection (Figs. 735, 743).

Natural History, Distribution. A specimen of *H. chiriqui* was "collected to the side of orb—both specimens with a set of eggs under a leaf; in the orb at night (esp. dusk)" next to a stream in mountain forest (R. Buskirk letter, 27 June 1971). The type specimen of *H. chiriqui* came probably from a mud-dauber nest, and the large number of specimens available to Simon of *H. nigritarsis* may also have come from a mud-dauber nest.

KEY TO *HOMALOMETA* SPECIES

1. Males 2
– Females 3
2(1). Palpal tibia wider than long with a pointed lateral projection below spur (Fig. 743); Costa Rica, Panama ..... *chiriqui*
– Palpal tibia longer than wide, without lateral projection below spur (Fig. 735); Lesser Antilles, Mexico to Panama ..... *nigritarsis*
3(1). Openings of epigynum inside pockets on each side of swellings (Figs. 740–742); Costa Rica, Panama ..... *chiriqui*
– Openings of epigynum anterior or posterior on surface of swelling 4
4(3). Openings of epigynum facing posterior with visible portion of connecting duct anterior of opening (Fig. 747); southeastern Brazil ..... *nossa*
– Openings of epigynum facing anterior with connecting duct, if visible, behind openings (Figs. 731, 733); Lesser Antilles, Mexico to Panama ..... *nigritarsis*



Figures 731–739. *Homalometa nigritarsis* Simon. 731–733. Epigynum. 731, 733. Ventral. 732. Dorsal. 734. Female. 735–739. Left male palpus. 735, 737. Ventral. 736, 739. Dorsal. 738. Lateral. 731, 735, 736. (Syntypes). 732, 733, 737–739. (Panama).

Figures 740–746. *H. chiriqui* n. sp. 740–742. Epigynum. 740. Dorsal, cleared. 741. Ventral, cleared. 742. Ventral. 743–746. Male palpus. 743. Ventral. 744. Lateral. 745. Dorsal. 746. Mesal.

Figure 747. *H. nossa* n. sp., epigynum, ventral.

Scale lines. 0.1 mm, except Figure 734, 1.0 mm.

Homalometa nigritarsis Simon
Figures 731–739; Map 5

Homalometa nigritarsis Simon, 1897: 872. Eight female, one male, 9 immature, syntypes in poor condition from St. Vincent Island, Lesser Antilles (BMNH) and female syntypes (MNHN), examined. Roewer, 1942: 914. Bonnet, 1957: 2230.

Description. Female. Carapace, ster-

num, legs yellowish. Abdomen with white pigment, center of dorsum without pigment (Fig. 734). Anterior median eyes twice their diameter apart, their diameter from laterals. Posterior median eyes 1.3 diameters apart, same distance from laterals. Abdomen subspherical. Total length, 3.0 mm. Carapace, 1.2 mm long, 0.9 mm wide. First femur, 1.3 mm; patella and tibia, 1.6 mm; metatarsus, 1.2 mm; tarsus, 0.6 mm. Second patella and tibia, 1.4 mm; third, 0.9 mm; fourth, 1.4 mm.

Male. Color like female. Anterior median eyes two diameters apart, 0.5 diameters from laterals. Posterior median eyes 1.5 diameters apart, one diameter from laterals. Clypeus height equal to two diameters of anterior median eyes. Total length, 1.5 mm. Carapace, 0.78 mm long, 0.78 mm wide. First femur, 1.1 mm; patella and tibia, 1.4 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.7 mm; fourth, 1.1 mm.

Variation. Total length of females varies from 2.5 to 3.3 mm. The Central American spiders lack the bald dorsal spot on the abdomen and are evenly covered by pigment.

Note. The male syntype is an individual just before a molt or just after (Figs. 735, 736). A second male from Panama has only one palpus which is slightly expanded (Figs. 737–739).

Diagnosis. The epigynum differs from that of *C. chiriqui* and *C. nossa* by having the openings lateral on each side, with palpal parts hanging in an anterior direction (Figs. 731–733).

Records. MEXICO *Est. Nayarit:* Tepic, 15 Sept. 1953, ♀ (B. Malkin, AMNH). PANAMA *Panamá:* Barro Colorado Isl., Gatun Lake, 20 Apr. 1953, ♂ (A. M. Nadler, AMNH); 1–6 Aug. 1959 (A. M. Chickering, MCZ). LESSER ANTILLES Martinique, 1967, 5♀ (Beatty, AMNH).

Homalometa chiriqui new species
Types 740–746; Map 5

Holotype. Female holotype, 3♀, 1♂, imm. paratypes from El Volcán, Prov. Chiriquí, Panama, 9–14 Aug. 1950 (A. M. Chickering, MCZ). The name is a noun in apposition after the Indian tribe and name of the province.

Note. The type specimens have an insect larva on each abdomen. The collection probably came from a mud-dauber nest. The male has only one palpus and has the palpal tibia separated from the cymbium and bulb, although they were placed together in Figures 745, 746.

Description. Female. Carapace, sternum, legs orange-white; abdomen and dorsum covered with white pigment spots which touch each other; no spots around pedicel and spinnerets. Narrow canoe-shaped tapetum of posterior median eyes shifted toward median of spider. Anterior median eyes 1.8 diameters apart, 1.5 diameters from laterals. Posterior median eyes 1.3 diameters apart, 2 diameters from laterals. Clypeus height equal to 1.7 diameters of anterior median eyes. Chelicerae with three teeth on posterior margin, the middle one small, many denticles in groove. Abdomen oval. Total length, 4.0 mm. Carapace, 2.0 mm long, 1.5 mm wide. First femur, 2.7 mm; patella and tibia, 3.5 mm; metatarsus, 2.8 mm; tarsus, 1.2 mm. Second patella and tibia, 2.7 mm; third, 1.7 mm; fourth, 2.4 mm.

Male. Color like female, but sternum darker and venter of abdomen dusky, except for a pair of white spots side by side behind epigastric furrow. Secondary eyes slightly smaller than anterior medians. Anterior median eyes 1.6 diameters apart, more than their diameter from laterals. Posterior median eyes 1.6 mm apart, 2 diameters from laterals. Clypeus height equal to almost twice diameter of anterior median eyes. Chelicerae oval with three teeth on anterior margin. Abdomen oval. Total length, 2.9 mm. Carapace, 1.6 mm long, 1.3 mm wide. First femur, 2.1 mm; patella and tibia, 2.7 mm; metatarsus, 2.3 mm; tarsus, 0.8 mm. Second patella and tibia, 2.1 mm; third, 1.3 mm; fourth, 1.7 mm.

Variation. Total length of females varies from 4.0 to 5.8 mm.

Diagnosis. The epigynum of this species

differs from that of *H. nigritarsis* by having the openings inside pockets on each side of a swelling (Figs. 740–742). The male palpus differs from others by having a tibia that is wider than long (Fig. 743), and by being larger in size (Figs. 743–746).

Natural History, Distribution. Specimens were collected to the side of orb (see above), Costa Rica to Panama.

Paratypes. Specimen from type collection placed in MIUP and AMNH. COSTA RICA. *Prov. San José:* Bajo La Hondura, 1,600 m, Oct. 1982, ♀ (W. Eberhard TL 40-3, MCZ). *Puntarenas:* Monteverde, 1,380 m, river edge and forest, 21 June 1971, 2♀ (W. R. Buskirk, MCZ); Dec. 1971, ♀, imm. (W. R. Buskirk, USNM).

Homalometa nossa new species
Figures 747; Map 5

Type. From Fazenda Nossa Senhora das Neves, Itamarajú, cacao plantation, Est. Bahia, Brazil, 9 Oct. 1978 (J. S. Santos, no. 11022, MCN). The specific name is a noun in apposition after the type locality.

Note. Specimen shriveled, in poor condition.

Description. Female. Carapace, clypeus, labium, sternum, legs brownish-yellow. Abdomen covered by white pigment spots except anterior of spinnerets and around pedicel. Anterior median eyes more than twice their diameter apart, their diameter from laterals. Posterior median eyes twice their diameter apart, same distance from laterals. Chelicerae with two teeth on posterior margin. Abdomen oval. Total length, 3.5 mm. Carapace, 1.4 mm long. First femur, 2.3 mm; patella and tibia, 2.8 mm; metatarsus, 2.3 mm; tarsus, 0.9 mm. Second patella and tibia, 2.3 mm; third, 1.3 mm; fourth, 2.1 mm.

Diagnosis. This species differs from *H. nigritarsis* by having longer legs and the openings of the epigynum more posterior (Fig. 747).

LITERATURE CITED

ARCHER, A. F. 1951. Studies in the Orbweaving Spiders (Argiopidae). I. Amer. Mus. Novitates, no. **1487:** 1–52.

———. 1958. Studies in the Orbweaving Spiders (Argiopidae). IV. Amer. Mus. Novitates, no. **1922:** 1–21.

BANKS, N. 1898. Arachnida from Baja California and other parts of Mexico. Proc. California Acad. Sci., ser. 3, **1:** 205–308.

———. 1909. Arachnida from Costa Rica. Proc. Acad. Natur. Sci., Philadelphia, **61:** 194–234.

BERLAND, L. 1913. Araignées in Mission du Service géographique de l'armée pour la mesure d'un arc du méridien equatorial en Amerique du Sud (1899–1906), Paris.

BLANKE, R. 1983. Behaviour as an indicator of taxonomic relationships in Arachnology (Arachnida: Araneae). Verh. naturwiss. Verein Hamburg, **26:** 217–226.

BONNET, P. 1956. Bibliographia Araneorum, Toulouse, **2:** 919–1926.

———. 1957. Bibliographia Araneorum, Toulouse, **2:** 1927–3026.

———. 1958. Bibliographia Araneorum, Toulouse, **2:** 3027–4230.

———. 1959. Bibliographia Araneorum, Toulouse, **2:** 4231–5058.

BRIGNOLI, P. M. 1983. A catalogue of the Araneae described between 1940 and 1981. Manchester Univ. Press, Manchester, 755 pp.

BROWN, F. M. 1941. A gazetteer of entomological stations in Ecuador. Ann. Entomol. Soc. Amer., **34:** 809–851.

BRYANT, E. B. 1940. Cuban spiders in the Museum of Comparative Zoology. Bull. Mus. Comp. Zool., **86:** 247–554.

———. 1942. Additions to the spider fauna of Puerto Rico. J. Agric., Univ. Puerto Rico, **26:** 1–16.

———. 1945. The Argiopidae of Hispaniola. Bull. Mus. Comp. Zool., **95:** 357–422.

CAMBRIDGE, F. P.- 1898. On some spiders from Chili and Peru, collected by Dr. Plate of Berlin. J. Linn. Soc. London, **27:** 15–22.

———. 1903. Arachnida, Araneidea, **2:** 425–464. *In* Biologia Centrali-Americana. Zoologia. London.

CAMBRIDGE, O. P.- 1889. Arachnida, Araneidea, **1:** 1–56. *In* Biologia Centrali-Americana. Zoologia. London.

———. 1894. Arachnida, Araneidea, **1:** 121–144. *In* Biologia Centrali-Americana. Zoologia. London.

———. 1896. Arachnida, Araneidea, **1:** 161–224. *In* Biologia Centrali-Americana. Zoologia. London.

———. 1899. Arachnida, Araneidea, **1:** 289–304. *In* Biologia Centrali-Americana. Zoologia. London.

CAPORIACCO, L. DI 1947. Diagnosi preliminari delle specie di aracnidi della Guiana Brittanica raccolte da Beccari e Romiti. Monti. zool. ital., **56:** 20–34.

———. 1954. Araignées de la Guyane Française

du Muséum d'Histoire Naturelle de Paris. Comment. Pontif. Acad. Sci., **16:** 45–193.

CHAMBERLIN, R. V. 1916. Results of the Yale Peruvian Expedition of 1911. The Arachnida Bull. Mus. Comp. Zool., **60:** 177–299.

CODDINGTON, J. 1986. The monophyletic origin of the orb-web. *In* W. A. Shear (ed.), Spider Webs and Spider Behavior. Stanford Univ. Press.

EBERHARD, W. 1982. Behavioral characters for the higher classification of orb-weaving spiders. Evolution, **36:** 1067–1095.

FORSTER, R. R., AND PLATNICK, N. I. 1984. A review of the archaeid spiders and their relatives, with notes on the limits of the superfamily Palpimanoidea (Arachnida, Araneae). Bull. Amer. Mus. Natur. Hist., **178:** 1–106.

FRANGANILLO BALBOA, P. 1930. Arácnidos de Cuba. Inst. Nac. Invest. Cien., **1:** 47–99.

———. 1936. Los Arácnidos de Cuba hasta 1936. La Habana, 180 pp.

GERHARDT, U. 1921. Vergleichende Studien über die Morphologie des männlichen Tasters und die Biologie der Kopulation der Spinnen. Arch. Naturgesch., **87:** 78–247.

———. 1923. Weitere sexualbiologische Untersuchungen an Spinnen. Arch. Naturgesch., **89:** 1–225.

———. 1924. Weitere Untersuchungen über die Biologie der Spinnen. Arch. Naturgesch, **90:** 85–192.

———. 1933. Neue Untersuchungen zur Sexualbiologie der Spinnen. Z. Morphol. Ökol. Tiere, **27:** 1–75.

HELVERSON, O. VON 1976. Gedanken zur Evolution der Paarungstellung bei den Spinnen (Arachnida: Araneae). Entom. Germanica, **3:** 13–28.

HOLM, Å. 1940. Studien über die Entwicklung und Entwicklungsbiologie der Spinnen. Zool. Bidr., **19:** 1–214.

HOMANN, H. 1952. Die Nebenaugen der Araneen. Zool. Jahrb. Abt. Anat. Ontog. Tiere, **72:** 345–364.

KASTON, B. J. 1948. Spiders of Connecticut. Bull. State Geol. Nat. Hist. Surv., **70:** 1–874.

KEYSERLING, E. 1863. Beschreibungen neuer Spinnen. Verh. Zool.–Bot. Gesell. Wien, **13:** 369–382.

———. 1865. Beiträge zur Kenntnis der Orbitelae Latr. Verh. Zool.–Bot. Gesell. Wien, **15:** 799–856.

———. 1878. Spinnen aus Uruguay und einigen anderen Gegenden Amerikas. Verh. Zool.–Bot. Gesell. Wien, **27:** 571–624.

———. 1880. Neue Spinnen aus Amerika. Verh. Zool.–Bot. Gesell. Wien, **29:** 293–349.

———. 1881. Neue Spinnen aus Amerika. II. Verh. Zool.–Bot. Gesell. Wien, **30:** 547–582.

———. 1881. Neue Spinnen aus Amerika. III. Verh. Zool.–Bot. Gesell. Wien, **31:** 269–314.

———. 1883. Neue Spinnen aus Amerika. IV. Verh. Zool.–Bot. Gesell. Wien, **32:** 195–226.

———. 1884. Neue Spinnen aus Amerika. V. Verh. Zool.–Bot. Gesell. Wien, **33:** 649–684.

———. 1893. Die Spinnen Amerikas. Epeiridae. Nürnberg, **4:** 209–377.

KRANTZ, G. W. 1978. A Manual of Acarology, second edition. Oregon State Univ. Book Stores, Inc., Corvallis, pp. 88–89.

LEDOUX, J.-C. 1985. La position systématique de *Sedasta ferox* Simon (Araneae, Argiopidae). Rev. Arachnol., **6:** 71–80.

LEVI, H. W. 1963. The American spider genera *Spintharus* and *Thwaitesia* (Araneae: Theridiidae). Psyche, **70:** 223–234.

———. 1974. The orb-weaver genus *Zygiella*. Bull. Mus. Comp. Zool., **146:** 291–316.

———. 1978. The American orb-weaver genera *Colphepeira*, *Micrathena* and *Gasteracantha* north of Mexico (Araneae, Araneidae). Bull. Mus. Comp. Zool., **148:** 417–442.

———. 1980a. The orb-weaver genus *Mecynogea*, the subfamily Metinae and the genera *Pachygnatha*, *Glenognatha* and *Azilia* of the subfamily Tetragnathinae north of Mexico. Bull. Mus. Comp. Zool., **149:** 1–74.

———. 1980b. Orb-webs: Primitive or specialized? Proc. 8th Internat. Congr. Arachnol. Wien, pp. 367–370.

———. 1981. The American orb-weaver genera *Dolichognatha* and *Tetragnatha* north of Mexico. Bull. Mus. Comp. Zool., **149:** 271–318.

———. 1982. Araneae. *In* S. P. Parker (ed.), Synopsis and Classification of Living Organisms. McGraw–Hill Book Co., New York, **2:** 77–95.

———. 1985. The spiny orb-weaver genera *Micrathena* and *Chaetacis* (Araneae, Araneidae). Bull. Mus. Comp. Zool., **150:** 429–615.

LOCKET, G. H., A. F. MILLIDGE, AND P. MERRETT. 1974. British Spiders. Ray Soc., **3:** 1–315.

MELLO–LEITÃO, C. F. 1941. Las Arañas de Cordoba, La Rioja, Catamarca, Tucuman, Salta y Jujuy. Rev. Mus. La Plata, **2:** 99–198.

———. 1944. Arañas de la Provincia de Buenos Aires. Rev. Mus. La Plata, **3:** 311–393.

MENGE, A. 1866. Preussische Spinnen. Schrift. Naturf. Gesell. Danzig, **1:** 1–152.

NICOLET, H. 1849: 491. Arácnidos. *In* Gay, C. Historia física y política de Chile. Zoologia, **3:** 319–543.

PETRUNKEVITCH, A. 1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands. Bull. Amer. Mus. Natur. Hist., **29:** 1–791.

———. 1930. The spiders of Porto Rico. Trans. Connecticut Acad. Arts Sci., **30:** 159–355.

ROBINSON, M., AND B. ROBINSON. 1980. Comparative studies of the courtship and mating behavior of tropical araneid spiders. Pacific Insect Monogr., **36:** 1–218.

ROEWER, C. F. 1942. Katalog der Araneae. Bremen.

SIMON, E. 1895. Histoire Naturelle des Araignées, Paris, **1:** 761–1084.

———. 1897. On the spiders of the Island of St. Vincent. Proc. Zool. Soc. London, **1897:** 860–890.

———. 1900. Liste des Arachnides recueillis par M. Ch. E. Porter en 1898-1899 et descriptions d'espèces nouvelles. Rev. Chil. Hist. Nat., **4:** 49–55.

———. 1901. Liste des Arachnides recueillis par M. Ch. E. Porter en 1899 à Quilipué et à Molle et par M. B. Wilson en avril 1900 au Rio Aysen Patagonia occidentale. Rev. Chil. Hist. Nat., **5:** 17–22.

———. 1902. Arachniden, excl. Acariden und Gonyleptiden in Ergeb. Hamburger Maggalhaensische Sammelreise. Hamburg, **6:** 1–47.

———. 1929. Les Arachnides de France. Paris, **6:** 643–1298.

SOARES, B. A. M., AND H. F. CAMARGO. 1948. Aranhas coligidas per la fundação Brasil Central. Bol. Mus. Para. Emilio Goeldi, **10:** 355–409.

———. 1955. Algumas novas especies de aranhas brasileiras. Arch. Mus. Nac. Rio de Janeiro, **42:** 577–580.

STRAND, E. 1915. Systematische-faunistische Studien über paläarktische, afrikanische und amerikanische Spinnen des senckenbergischen Museums. Arch. Naturgesch., **81A:** 1–153.

TACZANOWSKI, L. 1873. Les Aranéides de la Guyane française. Horae Soc. Entomol. Ross., **10:** 56–115.

TULLGREN. A. 1902. Spiders collected in the Aysen Valley in South Chile by Mr. P. Dusén. Bih. Svenska Vet. Akad. Handl., **28:** 1–77.

———. 1905. Araneida from the Swedish Expedition through the Gran Chaco and the Cordilleras. Ark. Zool., **2**(19): 1–81.

TUZET, O., AND J.-F. MANIE. 1959. Recherches sur la Spermiogenèse des Araignées: *Araneus cornutus* Cl., *Tetragnatha pinicola* L. M., *Philodromus poecilus* Th. et *Chiracanthium* sp. Ann. Sci. Natur. Zool., ser. 12, **1:** 91–103.

WIEHLE, H. 1963. Tetragnathidae. *In* Die Tierwelt Deutschlands, **49:** 1–76.

———. 1967. *Meta*,—eine semientelegyne Gattung der Araneae. Senckenbergia Biol., **48:** 183–196.

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The Skull and Dentition of Two Tritylodontid Synapsids from the Lower Jurassic of Western North America

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THE SKULL AND DENTITION OF TWO TRITYLODONTID SYNAPSIDS FROM THE LOWER JURASSIC OF WESTERN NORTH AMERICA

HANS-DIETER SUES[1]

ABSTRACT. Based on an extensive collection of specimens from the Kayenta Formation (Lower Jurassic) of northeastern Arizona, a detailed anatomical account on the skull of two advanced non-mammalian synapsids referable to the family Tritylodontidae is presented. The material is referred to *Kayentatherium wellesi* D. M. Kermack, 1982 and *Dinnebitodon amarali* Sues, 1986, respectively; the skull of the latter form is still poorly known.

The upper postcanine teeth of *Kayentatherium* have two buccal, three median, and three lingual cusps whereas those of *Dinnebitodon* are distinguished by the presence of only two lingual cusps. *Kayentatherium* has but a single pair of upper incisors, which are enlarged and separated by an edentulous gap.

The presence of an internarial bar is demonstrated. The quadrate has a prominent stapedial process and articulates only with the crista parotica (anterior paroccipital process). The quadratojugal is a slender bony rod. The dentary has a very tall coronoid process with a distinctly recurved apex. The postdentary bones form a slender bony rod. The distinct retroarticular process consists of a thin central lamina and a posteriorly thickened rim. The postdentary elements were presumably involved in hearing and are extremely similar to the auditory ossicles in the most primitive mammals.

The skull bears prominent ectocranial crests and has deep zygomatic arches. The lateral wall of the braincase is completely ossified. An extensive secondary palate is formed by the maxillae and palatines in *Kayentatherium* and by the premaxillae and palatines in *Dinnebitodon*. A number of cranial features are consistent with the hypothesis that tritylodontid synapsids were herbivorous. Jaw motion was propalinal and included a significant, posteriorly directed power stroke.

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INTRODUCTION

The question of the origin of mammals has occupied the attention of several generations of anatomists and paleontologists. Extensive collections of advanced "mammal-like reptiles" and early mammals have been brought together from various regions of the world, and, although much detail remains to be clarified, the broader outlines of this important phase in the evolutionary history of the Synapsida are now slowly emerging. There exists a general consensus at present that mammals are derived from the Cynodontia, a paraphyletic assemblage of advanced synapsids of primarily Permian and Triassic age. Kemp (1982) and Jenkins (1984) have reviewed this subject most recently.

Certain Late Triassic and Jurassic representatives of this assemblage already show a host of mammalian characters and indeed have been referred to the Mammalia on occasion. Among these forms, the Tritylodontidae form a well-defined group, which is characterized principally by the possession of multicuspid molariform cheek-teeth that meet in precise occlusion. They were classified as primitive mammals with affinities to the Multituberculata by most authors until the 1940s. The discovery of well-preserved and abundant skeletal remains of Tritylodontidae in the Lower Lufeng Series of Yunnan, China (Young, 1940, 1947), now believed to be Early Jurassic in age, and in Liassic fissure-fillings in Somerset, England (Kühne, 1943, 1956) led to a revised assessment of the phylogenetic position of this group. Subsequently tritylodontids were regarded as highly derived descen-

dants of "gomphodont" cynodonts, combining a number of decidedly mammalian features with obvious specializations for herbivory (Watson, 1942; Crompton and Ellenberger, 1957). Recently, this view has been challenged by Kemp (1982, 1983) who argued for a sister-group relationship between Tritylodontidae and Mammalia (plus possibly Tritheledontidae). Elsewhere, I have reviewed arguments in support of both hypotheses (Sues, 1985a). I prefer the hypothesis that tritylodontids plus gomphodonts form a strictly monophyletic group, Tritylodontoidea (Hopson and Kitching, 1972). The discovery of numerous often admirably preserved and associated skeletal remains referable to three genera of Tritylodontidae from the "Silty Facies" of the Kayenta Formation in northeastern Arizona permits a comprehensive anatomical description of these advanced synapsids. Whatever their phylogenetic relationships may be, tritylodontids display a degree of structural organization comparable to or, in a number of features, even advanced beyond that of forms such as *Probainognathus*, which have commonly been hypothesized as members of the stem-group of the Mammalia. Clearly a detailed anatomical survey of the unusually well-documented Tritylodontidae from the Kayenta Formation is essential to a comprehensive evaluation of the interrelationships of advanced synapsids including mammals.

The present paper describes the skull and dentition in two species of Tritylodontidae from the Kayenta Formation, *Kayentatherium wellesi* D. M. Kermack, 1982 and *Dinnebitodon amarali* Sues, 1986. As anatomical descriptions are most meaningful when they relate skeletal features to soft structures, an attempt has been made to do so where the latter could be restored with a reasonable degree of confidence. Extant primitive mammals provided comparative information concerning neurovascular structures and cranial muscles for this purpose; such comparisons are, in my opinion, justified in view of the close relationships, regardless of the preferred hypothesis of tritylodontid affinities.

Most specimens show signs of crushing and other pressure effects, with consequent limitation on the accuracy with which individual illustrations and restorations can be prepared. For the same reasons, exact measurements are not feasible in most instances.

A second paper, in collaboration with F. A. Jenkins, Jr., will deal with the postcranial skeletons of *Kayentatherium* and *Dinnebitodon*. Elsewhere, I have already discussed the phylogenetic status of the Kayenta Tritylodontidae and their possible biostratigraphic significance (Sues, 1986b) and have described cranial remains and teeth referable to a third genus of Kayenta Tritylodontidae, *Oligokyphus* Hennig, 1922 (Sues, 1985b). The latter account includes remarks on jaws and teeth of juveniles presumably referable to *Dinnebitodon* and/or *Kayentatherium*.

The tritylodontid material from the Kayenta Formation collected by the Harvard-MNA field parties since 1977 has been divided between the Museum of Comparative Zoology, Harvard University (MCZ) and the Museum of Northern Arizona (MNA).

GEOLOGICAL BACKGROUND

Tritylodontid remains were first recovered from the Kayenta Formation in the early 1950s. This material was collected from 8 to 10 feet (2.4 to 3 m) below the top of the formation, just below the presumed contact with the Navajo Sandstone, on Comb Ridge, 6 miles (9.6 km) east of the type locality of the Kayenta Formation near Kayenta, Arizona (G. E. Lewis, 1986). These finds, recently referred to a new genus and species, *Nearctylodon broomi* Lewis, 1986, constituted the first record of this group of non-mammalian synapsids from North America. D. M. Kermack (1982) has described a poorly

preserved skull, the holotype of *Kayentatherium wellesi*, and some other jaw material from a locality near Many Farms, Apache County, Arizona, and a fragment of a very large tritylodontid dentary from Garces Mesa, Coconino County, Arizona. (It should be noted at this point that *Nearctylodon broomi* Lewis, 1986 is a subjective junior synonym of *Kayentatherium wellesi* D. M. Kermack, 1982; this synonymy will be discussed below.) The new specimens described in this paper were obtained from a number of sites in the "Silty Facies" in the middle third of the Kayenta Formation, exposed on Ward Terrace along the Adeii Eechii Cliffs on the land of the Navajo Indian Nation from the region of Dinnebito Wash to Tuba City. Locally these deposits are quite fossiliferous, especially near Gold Spring Wash, and contain a diversified fauna that, in addition to Tritylodontidae, mainly consists of an undescribed new taxon of turtle (Gaffney, Hutchinson and Jenkins, in preparation) and the small armored ornithischian dinosaur *Scutellosaurus lawleri* Colbert, 1981.

The Kayenta Formation is part of the Glen Canyon Group of western North America, a sequence of strata of continental sediments, which are primarily clastic in nature. The depositional basin of the Kayenta sediments, which accumulated on a well-drained lowland floodplain, extends in what are now the areas of northeastern Arizona and central and southern Utah. The source area for the deposits was probably situated in western Colorado, to the east or northeast of the Vermillion Cliffs. The sediments are predominantly red terrestrial and subaqueous claystones, sandstones, and siltstones. Clay pellet conglomerates and limestone form minor strata locally. Tracks of archosaurs, ripple-marked sandstones, and occasional mud-cracked surfaces attest to alternation between shallow water covering and subaerial exposure (Callahan, 1951: 54). The "Typical Facies" (Harshbarger *et al.*, 1957: 17) in the eastern part of the area is characterized by irregular ledges of sandstone and grades into the "Silty Facies," a sequence of intercalated claystones, sandstones, and siltstones, in the southwestern part of the Navajo country. The Kayenta Formation varies in thickness from 100 feet (30 m) at Lees Ferry to the east to more than 1,100 feet (330 m) in the Warner Range to the west. Harshbarger *et al.* (1957: 18) report large-scale intertonguing between the Kayenta Formation and the overlaying Navajo Sandstone in northern Arizona and southwestern Utah through an interval of up to 700 feet (210 m) and with a lateral extension for at least 100 miles (160 km). This led Lewis *et al.* (1961: 1439) to correlate the lower part of the Navajo Sandstone with the upper portion of the Kayenta Formation, which intertongues with it. Intertonguing has also been observed between the lower part of the Kayenta Formation and the Springdale Sandstone Member of the underlying Moenave Formation (Harshbarger *et al.*, 1957; profile on pl. 2), making them stratigraphical equivalents in several localities in northern Arizona. The two strata are virtually identical in their rock fabric and apparently had the same source and transport direction. Clark and Fastovsky (1986) provide additional geological information concerning the fossiliferous strata and stratigraphic sections at selected localities.

Following Peterson and Pipiringos (1979) and Olsen and Sues (1986), the Kayenta Formation is considered Early Jurassic, rather than Late Triassic, in age. Palynological data from the Whitmore Point Member of the Moenave Formation, which underlies the Kayenta, suggest that the latter is no older than late Sinemurian. The Glen Canyon Group is unconformably overlain by the marine sediments of the San Rafael Group, the oldest beds of which are early Bajocian in age. The biostratigraphical evidence afforded by the tritylodontid synapsids, particularly the presence of *Oligokyphus*, is consis-

tent with this assessment (Sues, 1985b, 1986b).

METHODS OF PREPARATION

The majority of specimens were prepared mechanically with the aid of carbide-steel needles and dental burrs of various sizes. Bones with a covering of hematite were partially treated by submersion in a 5 percent solution of $HSCH_2COOH$ (known under the trivial names of mercaptoacetic or thioglycolic acid). Already exposed bone was strengthened with a solution of polystyrene in ethylacetate. The fossils then were submerged in acid for approximately six hours, followed by approximately 18 hours of washing in running water. Softened hematite was removed with the aid of a small brush and fine needles. The procedure was repeated when necessary. Breaks were mended with commercial cyanoacrylate glues.

MATERIALS

The principal specimens used in the anatomical descriptions are two skulls referable to *Kayentatherium wellesi* on the basis of their upper dentition (MCZ 8811 and 8812). MCZ 8811 includes an incomplete but excellently preserved skull of a small individual, lacking most of the skull roof, the posterior portion of the right and virtually the entire left zygomatic arch, much of the braincase and the left quadrate and postdentary bones. The tip of the snout is not preserved, and the crowns of the enlarged upper incisors are partially broken off. The specimen has also been subject to some plastic distortion. The conspicuous texture on the bony surfaces of the snout, the presence of replacement incisors, and the rapid increase in buccolingual width of the postcanine teeth posteriorly, along with other features, attest to the immaturity of MCZ 8811. MCZ 8812 includes the virtually complete skull of a very large specimen, with an estimated skull length (measured along the ventral aspect) of *c.* 26 cm (MCZ 8811: *c.* 13.5 cm). Its principal preservational deficiency is considerable lateral crushing of the cranium, particularly affecting the basicranial, occipital, and palatal regions. Aside from its enormous size, maturity of the specimen is indicated by the lack of incisor replacement and a decrease in buccolingual width of the crowns on the posterior upper postcanine teeth.

In addition, other, more fragmentary cranial remains referable to *Kayentatherium* and the still poorly known *Dinnebitodon* were examined. A list of all specimens, including locality coordinates, has been provided by Sues (MS.). Institutional acronyms, preceding specimen numbers, are: MCZ, Museum of Comparative Zoology, Harvard University; MNA, Museum of Northern Arizona, Flagstaff; SAM, South African Museum, Cape Town; UCMP, Museum of Paleontology, University of California, Berkeley; USNM, National Museum of Natural History, Washington, D.C.

TERMINOLOGY

The following directional terms are used in the description of teeth: anterior, toward the front of the mouth; buccal, toward the side of the mouth (or cheek); lingual, toward the tongue; posterior, toward the back of the mouth. Otherwise standard anatomical nomenclature has been employed throughout the text.

ACKNOWLEDGMENTS

I am particularly indebted to F. A. Jenkins, Jr. for making available the splendid tritylodontid material obtained by field-parties under his direction. I acknowledge with gratitude discussions with E. F. Allin, A. W. Crompton, J. A. Hopson, F. A. Jenkins, Jr., K. F. Liem and especially R. Presley. J. A. Hopson, E. C. Olson, and R. Presley reviewed the manuscript. The cooperation and hospitality of the staff at various museums and research institutions greatly facilitated my comparative studies. I should like to thank A. J. Charig, M. Holloway, and A. Milner (London), G. E.

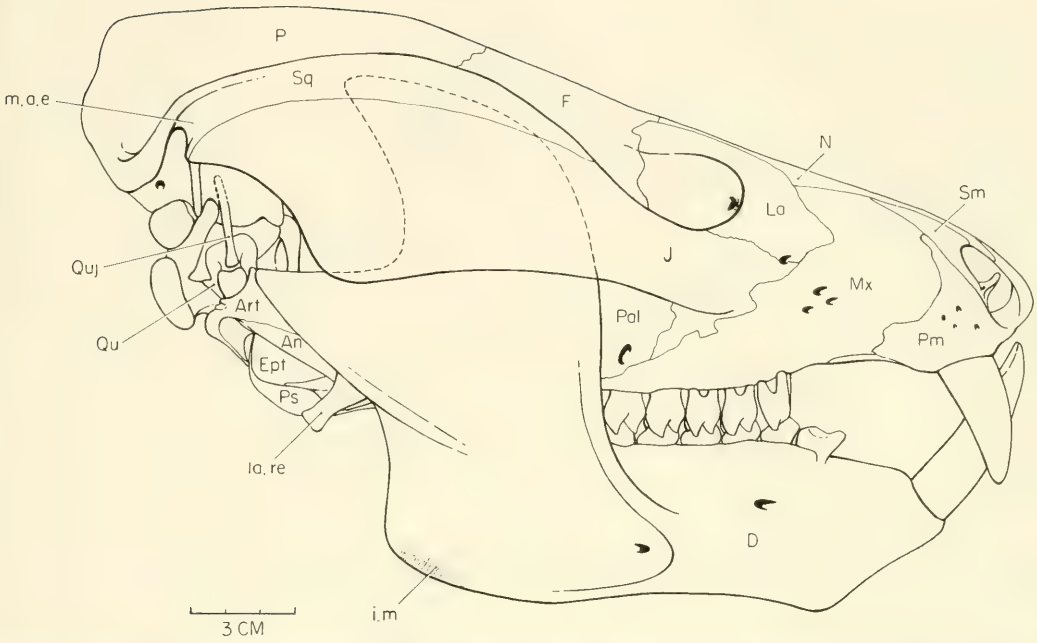

Figure 1. Skull of *Kayentatherium wellesi*, MCZ 8812. Right lateral view. Coronoid process indicated in broken line. *Abbreviations* for this and the following figures are listed at the end of the text under Appendix.

Lewis and T. M. Bown (Denver), K. A. Joysey (Cambridge), P. Wellnhofer (Munich) and F. Westphal (Tübingen). I owe a special debt of gratitude to A. J. and M. Charig for extending the generous hospitality of their home to me during an extended stay. I am much indebted to W. W. Amaral who has been instrumental during the often extremely difficult preparation of the specimens and who patiently taught me the skills of his craft. I also acknowledge the able assistance by A. H. Coleman (photography) and L. L. Meszoly (labelling).

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SKULL

The skull of *Kayentatherium* (Figs. 1, 2, 4 and 24) has a short and broad snout and a long and narrow postorbital region. The postorbital region of *Dinnebitodon* is apparently relatively shorter (MNA V3223) and its skull proportions are more closely comparable to those of *Bienotherium* as restored by Young (1947). The external nares are separated by an internarial bar. The prominent zygomatic arches enclose long and wide temporal fossae. The temporal fossae are broadly confluent anteriorly with the orbits, which

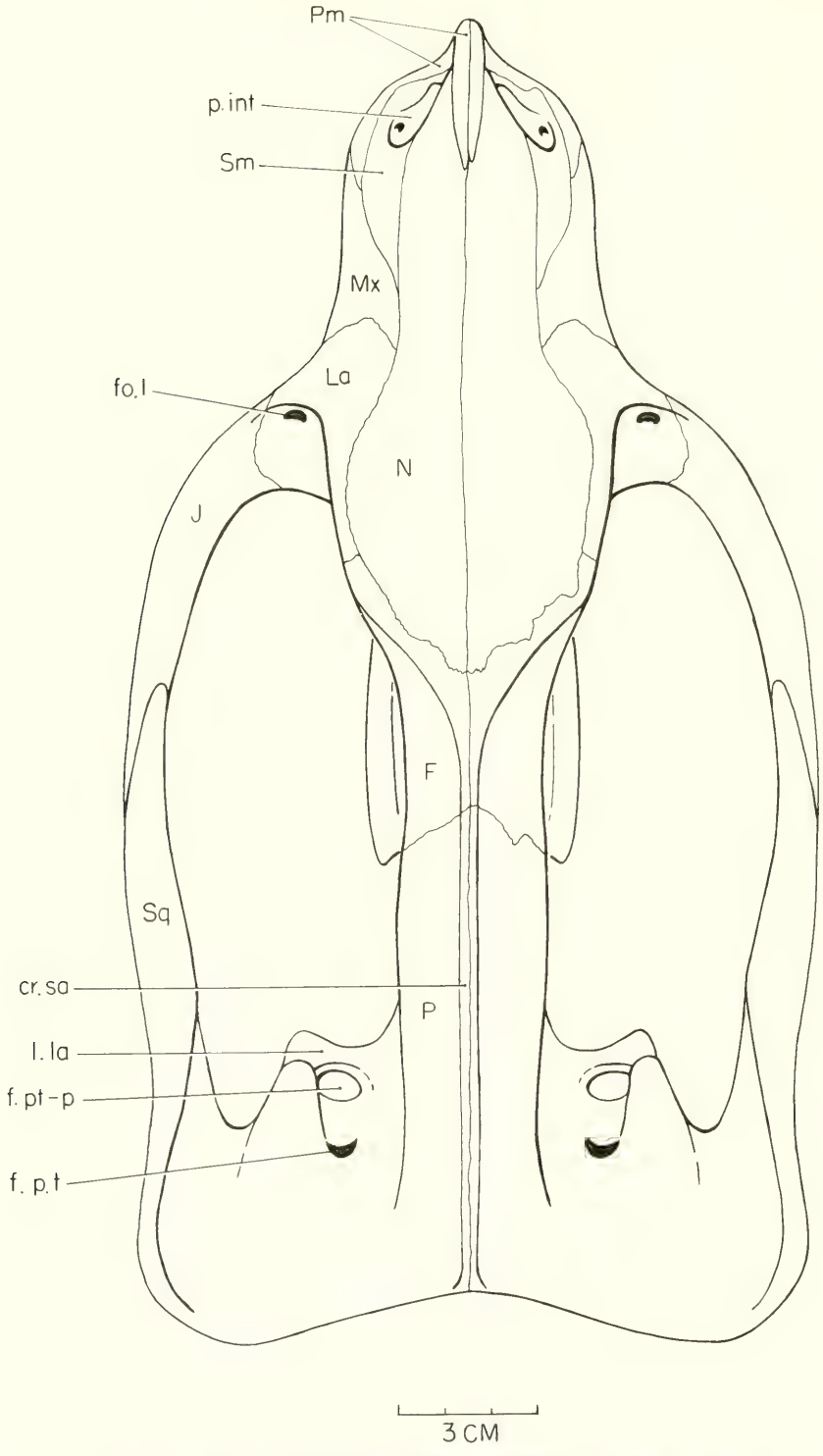


Figure 2. Skull of *Kayentatherium wellesi*, MCZ 8812. Dorsal view, restored.

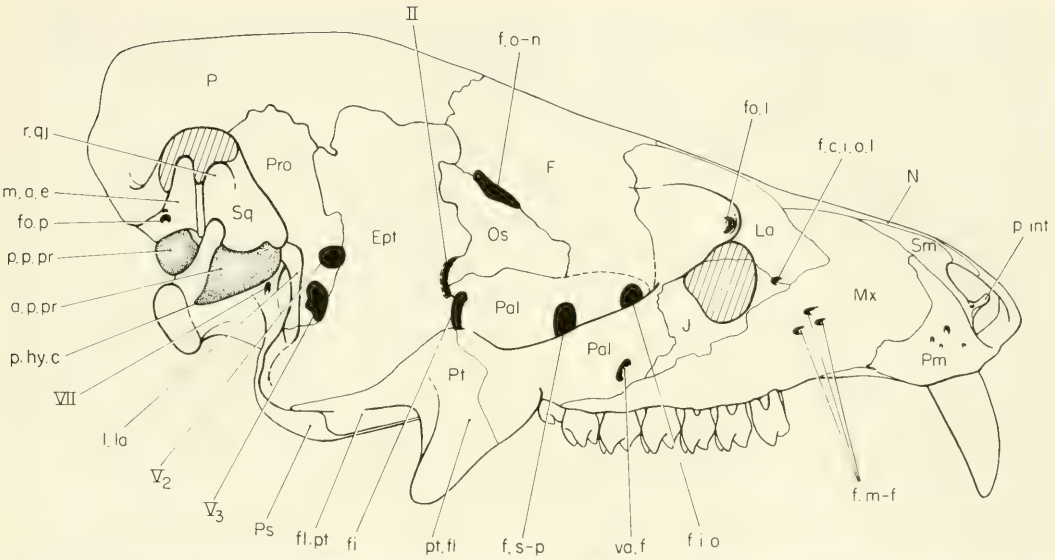


Figure 3. Skull of *Kayentatherium wellesi*, MCZ 8812. Right lateral view, with zygomatic arch and lower jaw removed. Unfinished distal surfaces on paroccipital process indicated by stippling.

are only delimited posterodorsally by bony knobs on the frontals. The posterior portion of the skull bears a distinct sagittal crest and posterolaterally diverging lambdoidal crests. A pineal foramen is absent. The broad and short snout of *Kayentatherium* tapers anteriorly and its sides diverge only little posteriorly. A well-developed secondary bony palate, formed by the maxillae and palatines, extends almost to the posterior end of the upper tooth row in *Kayentatherium* (Fig. 6). The posterior region of the palate shows a rather complex arrangement of longitudinal ridges and channels, reminiscent of that found in many non-therian mammals. The basicranium is broad posteriorly and triangular in ventral view, with the apex of this triangle directed anteriorly. The paroccipital process is robust and divided at its distal (lateral) end. Prominent occipital condyles, formed by the exoccipitals, are situated ventrolateral to the foramen magnum and are separated by a shallow notch for the robust dens. The broadly triangular occipital region is separated from the zygomatic arches laterally by a V-shaped notch on either side.

The lower jaw is characterized by a very large dentary with a tall and distinctly recurved coronoid process (Fig. 12). The postdentary bones are much reduced and form slender bony rods. They are lodged in a median sulcus on the dentary and articulate with a diminutive quadrate. The reflected lamina on the angular and the retroarticular process are well-developed.

Kayentatherium has one greatly enlarged lower incisor in each upper and lower jaw (Figs. 1, 4). In *Dinnebitodon* three (except two in MCZ 8836) upper incisors are developed, the second of which is enlarged (Sues, 1986a: fig. 1). A diastema separates the incisors in both genera from a row of precisely occluding postcanine teeth in both the upper and lower jaws.

Premaxilla (Pm). In lateral view, the anteroventral border of the premaxilla rises to form an internarial bridge with its fellow (Figs. 7, 8). The premaxilla is broadly overlapped posterolaterally by a flange from the maxilla as in *Oligokyphus* (Kühne, 1956: fig. 3C), and on the lateral border of the external narial opening it is covered by the large septomaxilla. The dorsolateral exposure of the bone is restricted to a narrow strip that ends in a posteriorly directed point and does not

reach the nasal above (although it extends about 12 mm further back on the left side of the face in MCZ 8812). This condition is comparable to the situation in *Tritylodon* (Simpson, 1928: fig. 1D: Ginsburg, 1962: fig. 4) but unlike *Bienotherium* as illustrated by Young (1947: figs. 1, 2). The palatal portion of the suture between premaxilla and maxilla is distinctly interdigitated. In MCZ 8811 (Fig. 6), the posterior sutural contact with the maxilla extends posteriorly between the first upper postcanine teeth but in the much larger specimen MCZ 8812 the suture extends well anterior to the cheek-teeth as in *Bienotherium* (Young, 1947: fig. 3). The condition in MCZ 8811 foreshadows that in *Dinnebitodon* (MCZ 8830, Fig. 25A) and in *Bienotheroides* (Sun, 1984: fig. 4) where premaxilla and palatine actually exclude the maxilla from participation in the formation of the secondary bony palate. The incisive foramina (f.inc, Fig. 6) are located between the enlarged upper incisors and are completely surrounded by the premaxillae; they were separated by "palatine" processes as in other synapsids. A distinct bony ridge, marking the lateral border of the palatal surface, extends from the enlarged upper incisor to the first postcanine tooth. It coincides with the lateral extent of the palatal portion of the suture between premaxilla and maxilla in *Kayentatherium*.

A slender internarial bar was formed by the long posterodorsal processes of the premaxillae (MCZ 8812; d.p.pm, Fig. 7). Previous authors described the external nares in the Tritylodontidae as confluent but, as is apparent from Young's (1947: 546) account, an internarial bridge was also developed in *Bienotherium*. Much of the posterodorsal processes is missing in the type of *B. yunnanense* but Young's figure 1 shows their posterior ends still wedged between the anterior ends of the nasals.

The sides of the premaxillae just behind the median internarial processes are excavated. The facial portion of the bone is convex anteroposteriorly as well as dorsoventrally and, in MCZ 8812, shows a number of tiny foramina. The sharp ventral margins of the premaxillae converge anteriorly and enclose between them a transversely concave, triangular area that extends onto the internarial bar anteriorly. The enlarged lower first incisors fit into this gap (Fig. 8).

The first incisor, present only in *Dinnebitodon*, is small and apparently pointed downward and forward. The second incisor is very large and projects more or less vertically downward as in *Bienotherium* (Young, 1947: fig. 2). The third incisor again is only developed in *Dinnebitodon* (with the apparent exception of MCZ 8836). It is much smaller than the preceding one and is situated posteromedial to the latter (Sues, 1986a: fig. 1).

Septomaxilla (Sm). The septomaxilla is a large element, overlying the anterior face of the premaxilla on the posterolateral margin of the external naris (Fig. 7). A septomaxillary foramen, commonly developed in more primitive synapsids such as *Procynosuchus* (Kemp, 1979: fig. 3), is absent. The septomaxilla contributes to the floor of the naris ventromedially and extends to the internarial septum as in *Tritylodon* (Simpson, 1928: fig. 1C). The septum nasi in *Tritylodon* (BMNH R8181) is not ossified but is preserved as a gray crystalline substance and was apparently formed in cartilage (Simpson, 1928: 12). This was presumably also the case in MCZ 8812.

A depression (d.p.i) is developed on the anterior surface of the medial portion of the septomaxilla, which forms part of the narial floor and a transverse wall in the posterior part of the naris. It is associated with the prominent shelf-like processus intrafenestralis of that bone (p.int, Fig. 7). Kemp (1979: 96 and fig. 10) has interpreted a similar feature in *Procynosuchus* as the site of Jacobson's organ. Romer and Price (1940: pl. 16, fig. A) place that organ on the posterodorsal aspect of the processus intrafenestralis of the septomaxilla in

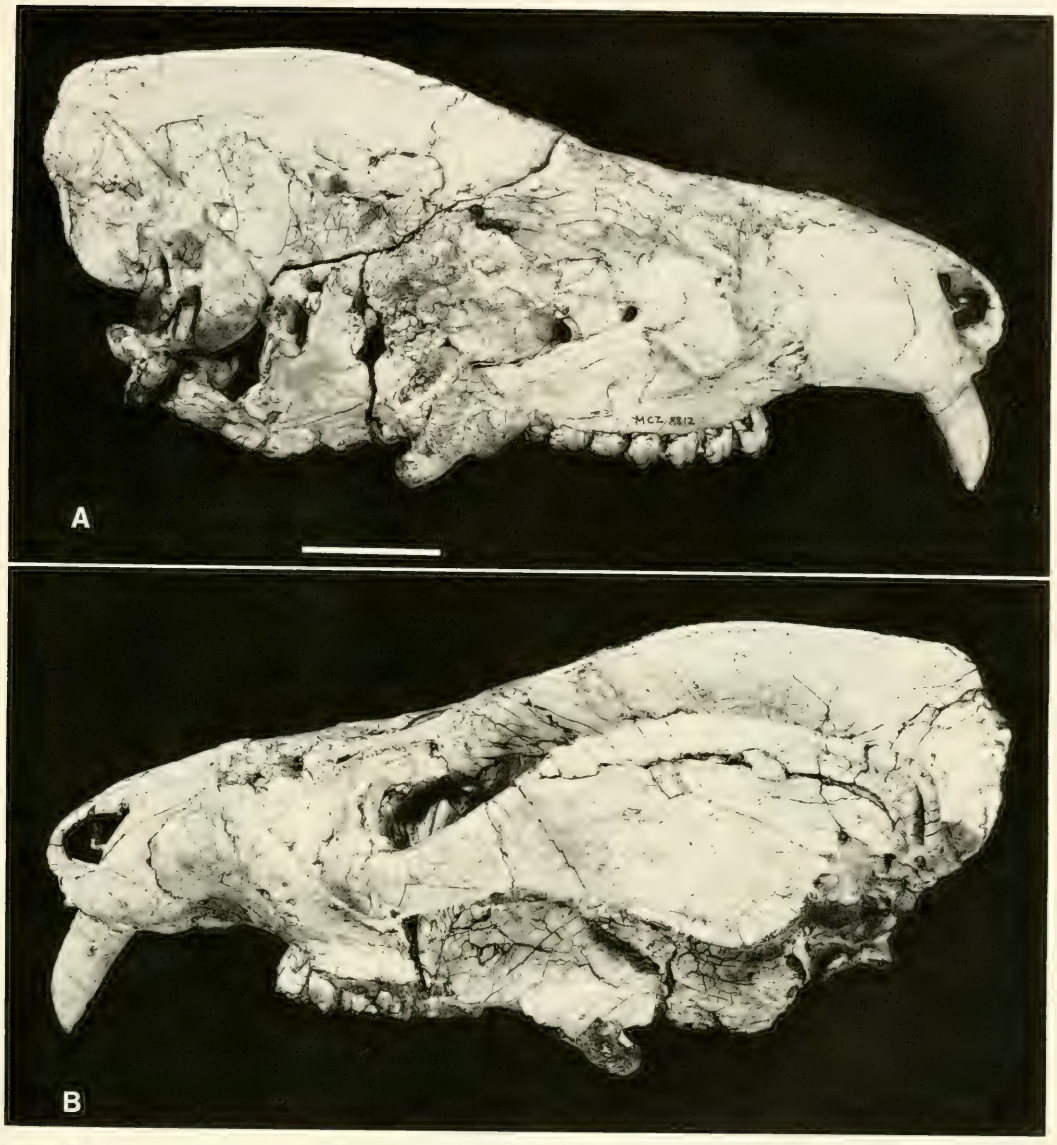


Figure 4. Skull of *Kayentatherium wellesi*, MCZ 8812. A) right lateral view without zygoma. B) left lateral view with zygoma and part of ascending ramus of dentary.

Scale bar. 4 cm.

Dimetrodon. This position is also more likely in the Tritylodontidae and, as in many extant mammals, Jacobson's organ may have extended back along the nasal septum (Presley, personal communication). A foramen (c.sm) opening into the transverse posterior wall of the depression is probably for a nasal branch of N. trigeminus. The processus intrafenestralis turns up as it approaches the mid-line. The elevated median ends of the processes from both sides enclose a space for the

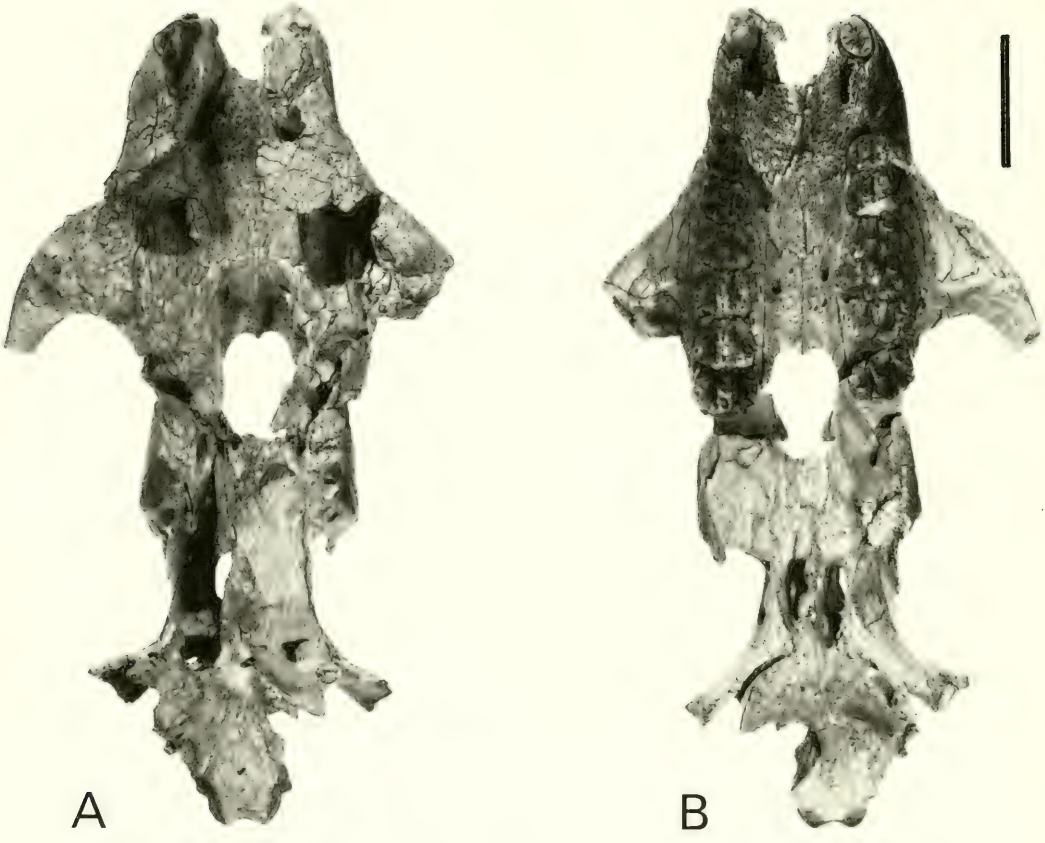


Figure 5. Skull of *Kayentatherium wellesi*, MCZ 8811. A) dorsal view. B) ventral view. *Scale bar.* 2 cm.

nasal septum (s.s.i). Near its lateral end, the process is obliquely traversed by a short, presumably vascular canal (fo.sm).

Maxilla (Mx). The maxilla is the most prominent bone in the facial skull in *Kayentatherium* (Fig. 1) but its lateral and palatal exposure in *Dinnebitodon* is much restricted. It underlies the jugal posterolaterally with a horizontal flange in *Kayentatherium*. The maxilla is overlapped posteromedially by a thin lamina from the palatine and posterodorsally and laterally by the expanded ventral base of the lacrimal. It has a rather short sutural contact with the nasal dorsally (MCZ 8812). The maxilla contacts the dorsal part of the extensive facial portion of the septomaxilla anterodorsally (Fig. 1). In *Dinnebitodon* (MCZ 8830), the jugal broadly overlaps the maxilla laterally and extends down almost to the level of the upper tooth row (Fig. 25B), much as in *Bienotheroides* (Sun, 1984: fig. 4).

The posterior portion of the maxilla is rather low and is quite thin around the posteriormost cheek-teeth and their roots (Fig. 4). The most conspicuous features of the extensive pars facialis of the maxilla in *Kayentatherium* are the maxillofacial foramina (see below). The bone is recessed anteriorly in front of the first postcanine tooth, probably to provide space for the crown of the forwardly rotated anteriormost tooth before shedding (Fig. 1); this feature is particularly pronounced in MCZ 8811 (mx.r, Fig. 6).

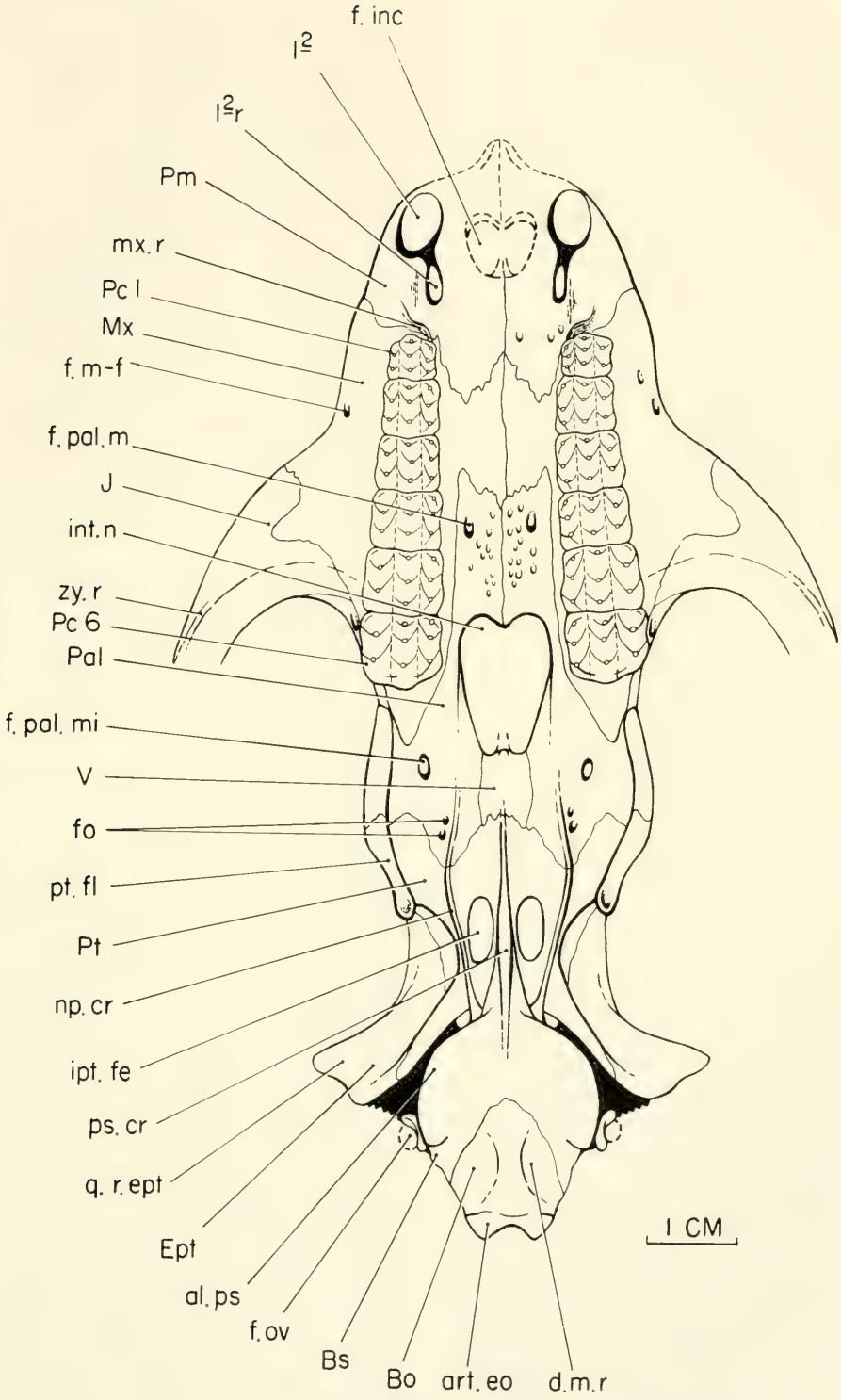


Figure 6. Skull of *Kayentatherium wellesi*, MCZ 8811. Partial reconstruction of skull in ventral view.

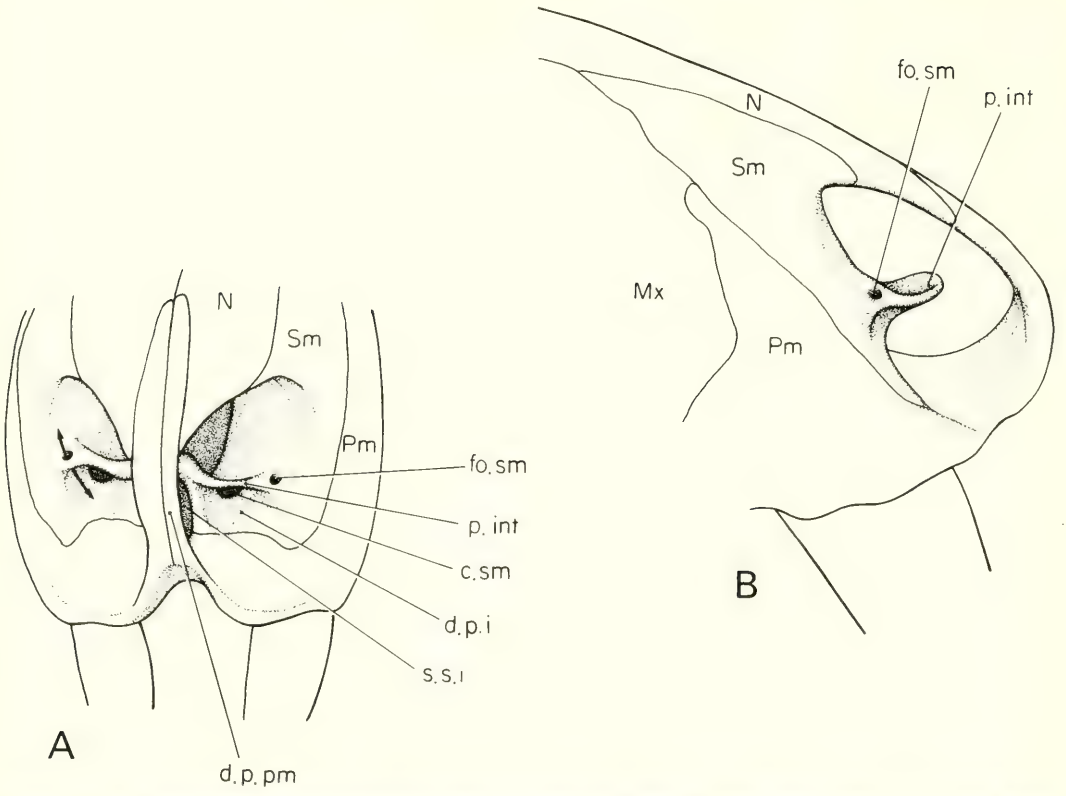


Figure 7. Circumnarial region of the snout in *Kayentatherium wellesi*, MCZ 8812. A) anterolateral view. B) right lateral view.

A large sinus maxillaris (si.mx, Fig. 9) is developed in the medial wall of the maxilla and occupies a position lateral to the entrance of the choana on the dorsal surface of the palate. It forms a deep recess in the inner wall of the maxilla and basal portion of the lacrimal, posterolaterally extending into the root of the zygoma. A partial thin median wall to the sinus is formed by the maxilla anteriorly and by the palatine more posteriorly. Branches of the infraorbital canal system extend on the floor of the sinus (c.i.o, c.i.o.l, Fig. 9). Similar sinuses have been documented in *Thrinaxodon* (Fourie, 1974: 349 and figs. 11A, 12, "MAN") and in *Luangwa* (Kemp, 1980: fig. 7B, "mx. sin.").

The tooth rows of the opposite maxillae are more or less parallel to each other and diverge only little posteriorly (relative to the mid-line; Figs. 5B, 6).

Infraorbital Canal System and Associated Structures. This most extensively developed neurovascular canal system to the snout is beautifully displayed in MCZ 8811, an immature specimen of *Kayentatherium*, where much of the skull roof has been eroded away (Figs. 5B, 9).

The canal for ramus maxillaris (V_2) of N. trigeminus extends obliquely between the sutural surfaces of the lacrimal and maxilla and continues forward on the floor of the maxillary sinus, much as in *Thrinaxodon* (Fourie, 1974: fig. 13B). At the level of the anterior end of the orbital fossa, it enters the snout (f.i.o, Fig. 3) and divides into an anteriorly extending larger branch and a much smaller lateral branch. The latter terminates in a small foramen (f.c.i.o.l, Fig. 3) above the sixth upper postcanine tooth on the suture between lacrimal and jugal. Kühne (1956: fig. 5A,

"L.V²") and Kermack *et al.* (1981: 17 and fig. 13, "f3") have observed similar lateral canals terminating on the suture between lacrimal and maxilla in *Oligokyphus* and *Morganucodon*, respectively. *Thrinaxodon* also shows a similar feature (Simpson, 1933: fig. 5). Up to three slit-like maxillofacial foramina (f.m-f, Fig. 3) are developed on the lateral aspect of the maxilla anteroventral to the orbit. They represent exits for branches of the large medial division of V_2 (as in *Oligokyphus*; Kühne, 1956: 27 and fig. 4A, "pEV²") and are homologous to the mammalian infraorbital foramen. Estes (1961: 175–177) has discussed the possible significance of neurovascular foramina on the lateral aspect of the maxilla in forms such as *Thrinaxodon*. He believed that their presence precluded the existence of movable muscular cheeks and lips. *Kayentatherium* shows a concentrated grouping of the maxillofacial foramina well above the alveolar margin, which, according to Estes, may well indicate the presence of a muscular cheek in this genus and other Tritylodontidae.

Posteriorly, N. trigeminus was presumably joined by the ramus palatinus of N. facialis (VII). A deep sulcus (s.v.n, Fig. 9) extends anterolaterally from the region of the vomer to the anterior margin of the orbital fossa. This groove is medially bordered by the orbital flange of the palatine and probably carried N. facialis to the sphenopalatine ganglion, together with various topographically related vessels. A similar groove in the early mammal *Morganucodon* (Kermack *et al.*, 1981: 55 and figs. 46B and D, 50, 100A, "g.Vid.ne") has been interpreted as carrying the Vidian nerve (i.e., ramus palatinus of VII). A small round pocket (MCZ 8811; d.g.s-p, Fig. 9) near the anterior end of the groove appears to represent the pterygopalatine fossa containing the sphenopalatine ganglion. This identification is supported by the presence of a prominent foramen (f.s-p, Fig. 3) between the orbitosphenoid and the dorsal portion of the palatine, just medial and anterior to the pit, that undoubtedly represents a foramen sphenopalatinum. Kemp (1980: fig. 7, "sp.pal.f.") has identified this feature in *Luangwa* and Kermack *et al.* (1981: figs. 46–48, "sph.for.") in *Morganucodon*. The palatine branch of ramus maxillaris of V, carrying fibers from VII, would have emerged through this foramen, along with A. sphenopalatina. The nerve then probably continued in a shallow groove on the medial aspect of the posterior portion of the palate through the foramen palatinum majus onto the ventral surface of the bony palate (Fig. 6). The greater palatine foramen presumably also served as an exit for A. palatina major as in mammals.

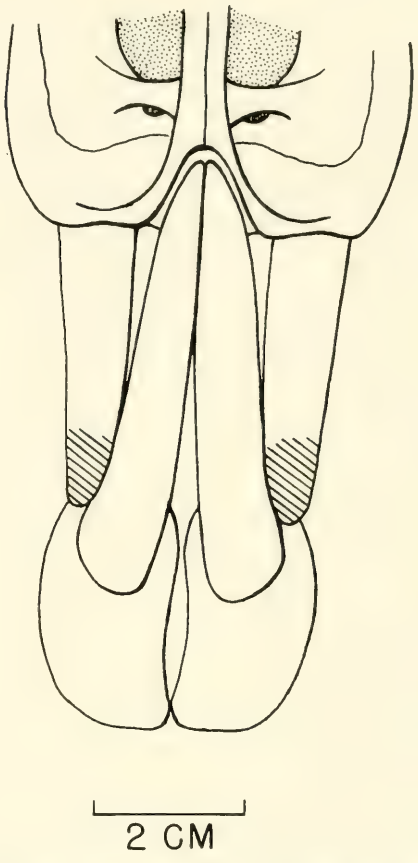


Figure 8. Anterior view of the snout in *Kayentatherium wellesi*, MCZ 8812, to show occlusal relationships of enlarged upper and lower incisors. Hatching denotes wear on upper incisor.

As described by Kühne (1956: 27 and

fig. 5D, "E.L.D.") in *Oligokyphus*, the lacrimal duct ends on the inner side of the lacrimal bone in a funnel. Only a single lacrimal foramen (fo.l, Figs. 3, 9) is present behind the ridge marking the anterior terminus of the orbit. In *Oligokyphus*, as in other cynodont synapsids, the lacrimal duct has two posterior foramina (Kühne, 1956: fig. 5) but only one foramen is present in *Tritylodon* (Simpson, 1928: fig. 1D). The feature called "lachrymal foramen" on the type skull of *Bienotherium yunnanense* (Young, 1947: 547) is obviously misidentified and, if not a mere artifact, probably represents a maxillofacial foramen.

A third canal system is associated with the infraorbital canal but apparently lacks any definite anatomical relation to it. It has also been noted in *Oligokyphus* by Kühne (1956: fig. 5, "Va.") and was interpreted by him as vascular in nature; furthermore, it is present in *Tritylodon* (Broili and Schröder, 1936: 190). A short canal extends posterodorsally from the posteroventral corner of the orbit on the posterolateral aspect of the palatine in both MCZ 8811 and 8812 (va.f, Figs. 3, 9).

Nasal (N). The nasal (Fig. 2) is long, flat, and relatively thin. It is narrow anteriorly where it forms the dorsal margin of the external narial opening but becomes much expanded posteriorly between the orbits, comparable to the condition in *Tritylodon* (Simpson, 1928: fig. 1B) and in *Bienotherium* (Young, 1947: fig. 1). Its posterior suture with the frontal is strongly interdigitated.

Frontal (F). The most prominent feature of the (in dorsal view) roughly triangular frontal is the median sagittal crest (cr.sa, Fig. 2). It divides anteriorly into two orbital ridges, each of which extends to the anterolateral corner of the frontal to form a rounded postorbital eminence, much as in *Bienotherium* (Young, 1947: fig. 1). The ridges enclose a smooth, flat to gently concave trigon between them. The frontal forms the dorsal rim to and part of the bony wall of the orbit. Both frontals form a median crest along the ventral surface near their anterior termini, which presumably supported the internasal septum (Tatarinov, 1963: 84). A distinct parasagittal crest, probably for the nasoturbinal (Tatarinov, 1963: 83), is developed on either side of the median ridge.

Parietal (P). The sagittal crest reaches its greatest depth on the parietal (Figs. 1, 4). The lambdoidal crests extend posterolaterally and ventrally. The slope of the lateral flange of the parietal is steeply vertical. The parietal is quite long anteroposteriorly and is overlapped ventrolaterally by thin dorsal lappets of the epipterygoid and prootic (MCZ 8812, Figs. 3, 4).

Lacrimal (La). The lacrimal (Fig. 3) has an extensive basal portion, which is suturally firmly attached to the maxilla and jugal below, a more dorsolaterally situated part that forms the anterior rim to and the anterolateral wall of the orbit, and has an extensive facial exposure. The bone is penetrated by the infraorbital canal system (see above) near its base and, more dorsally, by the lacrimal duct. The lacrimal sutures in *Dinnebitodon* (MCZ 8830) are very strongly interdigitated, and the lacrimal may have contacted the premaxilla anteriorly as in *Bienotheroides* (Sun, 1984: fig. 3), to the exclusion of the maxilla from the side of the face.

Jugal (J). The jugal (Fig. 1) is long and gently curved outward. It arises anteriorly at about the level of the first or second upper postcanine tooth. Its more posterior portion is formed by a deep, nearly vertical, and thin sheet of bone. It further increases in height toward the posterior end where it meets the squamosal along a long, oblique suture. More anteriorly, the squamosal overlaps the jugal laterally, but further posteriorly along the suture, the jugal fits into a groove on the ventral aspect of the squamosal (MCZ 8812). Toward the anterior end of the zygomatic arch (Fig. 1), the jugal rapidly decreases in height and becomes more robust and very wide transversely. Its lateral surface continues the outward curvature of the

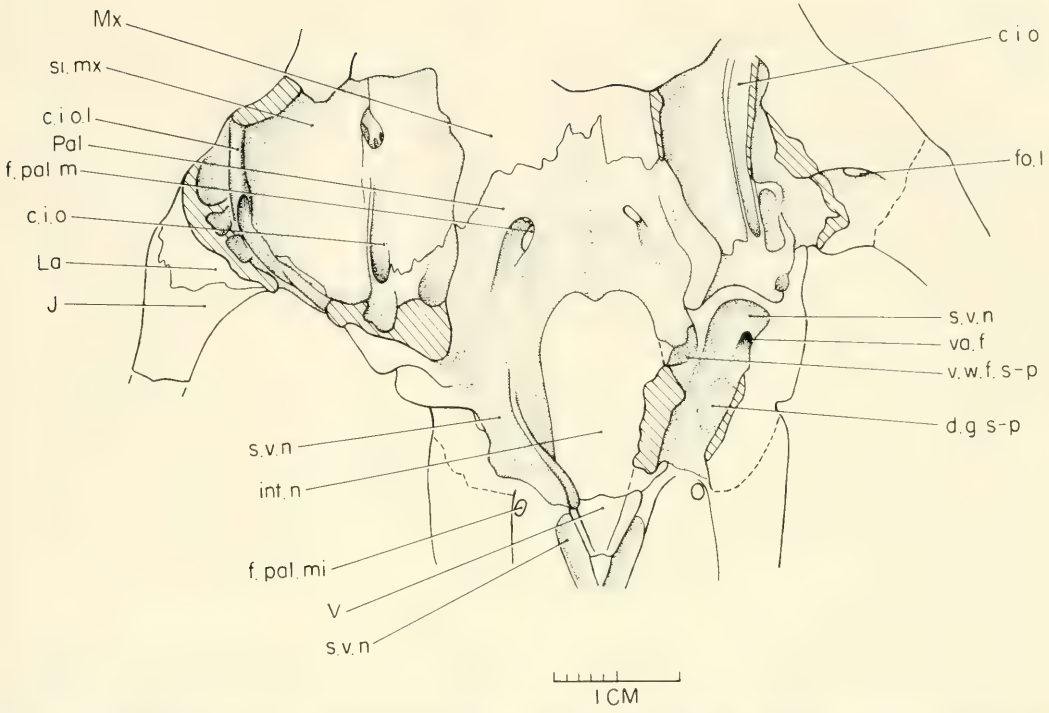


Figure 9. Maxillary sinuses and infraorbital canal system in the snout of *Kayentatherium wellesi*, MCZ 8812, in dorsal view.

bone whereas the dorsal edge turns medially. The anterior root of the zygoma is trihedral in transverse section. Its ventral aspect bears a distinct ridge (zy.r, Fig. 6), probably for the insertion of the pars superficialis of M. masseter and homologous to the suborbital process in the tritylodontoids *Exaeretodon* (Bonaparte, 1962: fig. 4) and *Trirachodon* (Crompton, 1963: fig. 10).

Squamosal (Sq). The cranial and zygomatic portions of the squamosal (Fig. 2) are separated by a depression that extends from the V-shaped notch in the posterolateral corner of the zygomatic arch to the region above the prominent crista parotica. The dorsal edge of the cranial process, corresponding to the mammalian crista lambdoidea, extends obliquely posteroventrally to the V-shaped notch and overhangs the occipital plate. The cranial part forms the dorsolateral margin of the post-temporal fenestra anteriorly. Cranial and zygomatic process join along a broad contact (Fig. 2). The zygomatic portion is quite deep (Fig. 1).

The rounded posterodorsal margin of the zygomatic process overhangs a distinct but rather narrow sulcus that extends along the posterolateral aspect of the squamosal (m.a.e, Figs. 1, 22). This groove expands posteroventrally, resulting in a hollow on the ventral aspect of the posterior zygomatic root. This depression is delimited by the posterolateral portion of the squamosal behind, by the crista parotica (anterior paroccipital process) anteromedially, and a low ridge, which separates it from a large pocket for the proximal end of the quadratojugal, anteriorly. One (MCZ 8842) or two (MCZ 8812, right side) foramina are developed near the posterior margin of the hollow (fo.p, Fig. 3). The squamosal sulcus (m.a.e) probably housed an external

auditory meatus as commonly restored in non-mammalian synapsids (Gregory, 1910: figs. 1, 2; Watson, 1911: figs. 1, 3, "Ex.Au.M."; Kühne, 1956: fig. 10B). Following Presley (1977), I assume that the meatus carried on forward and below from the ventral termination of the bony sulcus (Fig. 22). Just lateral to the crista parotica, a deep pit is developed on the ventral aspect of the squamosal (r.qj); following Kühne (1956: fig. 10B), it is interpreted as a recess for the proximal end of the quadratojugal. An anterior flange of the squamosal overlies the crista parotica (Fig. 3).

Quadrate (Qu). The quadrate (Fig. 10) is essentially similar to that of *Oligokyphus* (Kühne, 1956: fig. 9) and *Bienotherium* (Hopson, 1966: fig. 5B). The lateral margin of the quadrate is rounded, not truncated as in *Oligokyphus*, and slightly depressed above the trochlea for contact with the distal end of the rod-like quadratojugal. The trochlea (t.q) is transversely oriented and its articular surface extends onto the anterior aspect of the quadrate. The medial margin of the quadrate is drawn out into a long, tapering, and distinctly posteromedially curved process (m.p.q, Fig. 10), which is deeply excavated anteriorly. This deep anterior recess (st.f) presumably received the distal end of the stapes (Kühne, 1956: 39). Below the groove a distinct facet extends from the medial end of the trochlea to the medial extremity of the stapedial process. The proximal portion of the quadrate is formed by a horizontally expanded, smoothly concave, and upward facing sheet of bone (d.la) that is confluent with the medial surface of the posterodorsal process. The latter process is peg-like and relatively much shorter than that in *Oligokyphus*. A tubercle (a.q.f, Fig. 10A) is formed on the anteromedial margin of the expanded proximal portion immediately above the lateral end of the stapedial groove. It is comparable to the "anterior quadrate buttress" described in *Morganucodon* (Kermack *et al.*, 1981: 105) and may have served as the point of attachment for a ligament. The quadrate only contacted the massive crista parotica (anterior paroccipital process; Crompton, 1964: figs. 6, 8); the same mode of quadrate attachment developed apparently independently in *Morganucodon* and related forms (Crompton and Sun, 1985: 106 and fig. 4C). Comparisons with *Cynognathus* and *Diademodon* suggests that as the squamosal withdrew from the lateral surface of the paroccipital process the bulbous crista parotica extended laterally to form the sole contact with the quadrate (cf. Crompton, 1964: figs. 16, 17).

Kermack *et al.* (1981: 105) emphasize the similarity between the quadrates of *Morganucodon* and *Oligokyphus*. The quadrate of *Kayentatherium* is less similar to that of *Morganucodon*, especially in the prominent development of the stapedial process.

Quadratojugal (Quj). The quadratojugal (Fig. 1) is a splint-like bone, which is situated lateral to the quadrate and in close but loose contact with it (MCZ 8812). Its proximal end projects into an anterior pocket on the ventral aspect of the posterior zygomatic root.

Palatine (Pal). The extensive horizontal processes of the palatines (Figs. 5, 6) form the posterior portion of the extensively developed secondary palate and the crista choanalis in *Kayentatherium*. The palatine also forms a thin vertical plate of bone, which is closely applied to the medial surface of the maxilla on the sides of the internal nares above the level of the secondary palate. It excludes the maxilla from contact with the pterygoid and ascends to form much of the ventral part of the bony wall to the orbit. Posteriorly, the palatines form a short but distinct spina nasalis posterior (MCZ 8811) for the attachment of the raphe palati (aponeurosis of the palate) as in mammals. The straight lateral sutures anteriorly extend almost parallel to the mid-line suture. The anterior transverse suture between the palatine and maxilla in *Kayentatherium* is strongly serrated and extends posteromedially.

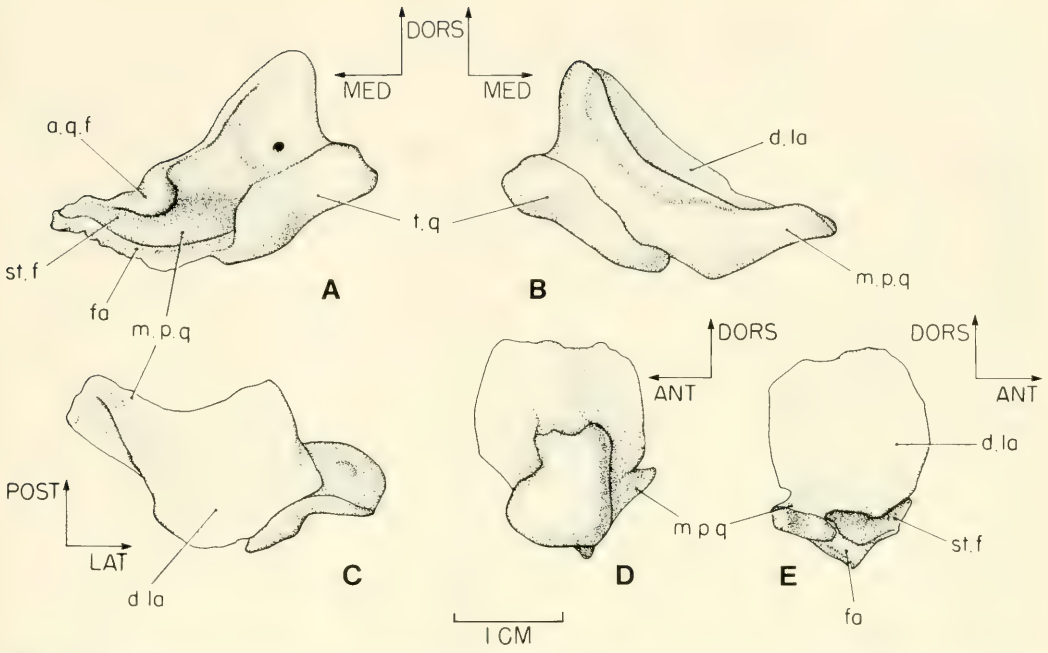


Figure 10. Left quadrate of *Kayentatherium wellesi*, MCZ 8812, oriented in approximate original position. A) anterior view. B) posterior view. C) dorsal view. D) lateral view. E) medial view.

The greater palatine foramen (f.pal.m) lies entirely within the palatine bone on both the dorsal and ventral surfaces of the secondary palate (Figs. 5, 6). It is clearly homologous to the mammalian foramen palatinum majus, which transmits A. palatina major and the palatine branch of V_2. Numerous minute pits are associated with it in MCZ 8811 but do not penetrate the palatine. A short sulcus extends from the greater palatine foramen anteriorly onto the palatal aspect of the maxilla.

The palate bears a low median ridge or torus (Fig. 5B) that extends forward up to the incisive foramina on the ventral surface. A similar crest, the base of the septum nasi, is developed on the dorsal surface. The horizontal plate of the palatine bone is transversely concave on both its dorsal and ventral faces. Posteriorly, the palatine meets the maxilla laterally, dorsally, and medially, the lacrimal, and the orbitosphenoid. The dorsal portion of the palatine forms a wall to the infraorbital canal. A small foramen (f.pal.mi) lies posteromedial to the sixth upper postcanine and in front of the suture between the palatine and pterygoid in MCZ 8811 (Fig. 6). It is similar to a foramen in *Morganucodon* that Kermack *et al.* (1981: 56 and fig. 46, "le.pl.for.") interpret as a passage of the lesser palatine nerve. Foramina in this position are also known in *Exaeretodon* (Bonaparte, 1962: fig. 4) and in *Oligokyphus* (Kühne, 1956: fig. 18). Posteromedial to this foramen and just lateral to the pterygo-palatine crest, two additional foramina (fo, Fig. 6) are developed in MCZ 8811. A possibly homologous foramen has been illustrated in *Diademodon* (Watson, 1911: fig. 3). They may have formed exits for pharyngeal branches of the nerves and vessels from the pterygopalatine fossa supplying the dorsal portion of the nasopharynx. The posterior part of the palatine contacts the unpaired vomer medially. An ectopterygoid is lacking.

Pterygoid (Pt). The almost vertical lat-

eral flange (pt.fl, Fig. 6) of the pterygoid is distinctly hook-shaped in lateral view and extends well below the level of the upper postcanine dentition. MCZ 8812 has a relatively much smaller flange than MCZ 8811, indicating a pronounced decrease in relative size during ontogeny (compare Figs. 3 and 11B). The convex lateral aspect of the flange is divided by a vertical ridge. Anterior to this ridge, the lateral surface of the pterygoid and of the adjacent region of the palatine shows a distinctive vermiculate texture, which is composed of fine grooves, pits, and ridges, much as on the dorsomedial part of the coronoid (MCZ 8811). A similar sculpturing is also present on the pterygoid of *Oligokyphus* (Kühne, 1956: pl. 10, fig. 2c) and may indicate areas of attachment of specialized connective tissue. A small oval depression of uncertain significance is situated on the lateral aspect of the medially curved distal extremity of the lateral flange in MCZ 8811. The convex external surface of the pterygoid flange lies behind and slightly medial to the buccal row of cusps on the posterior postcanine teeth (Fig. 6). The internal face of the lateral flange is distinctly concave anteroposteriorly and dorsoventrally. A short posterior ramus of the pterygoid extends posterolaterally on the ventral aspect of the posterior extension of the epipterygoid; neither reaches the quadrate.

The medial edge of the pterygoid turns upward to approach the basipterygoid joint. The pterygoids form the anterior portion of a prominent keel along the ventral aspect of the cranium, commencing behind the vomer and continued posteriorly by the parasphenoid (ps.cr, Figs. 6, 11B). On either side of this keel and enclosing a median trough with it, there is a sharp bony crest (np.cr, Fig. 6) formed by the pterygoid posteriorly and extending onto the palatine anteriorly. This nasopharyngeal crest runs more or less parallel to the median keel and probably defined the lateral boundary of the ductus naso-pharyngeus whereas the median keel possibly formed the attachment for the median raphe for the pharyngeal constrictors. The pterygo-palatine crest encloses a lateral trough with the lateral flange of the pterygoid. The entire configuration of longitudinal crests very closely resembles the system of ridges and troughs on the posterior portion of the palate in certain non-therian mammals (Multituberculata: Kielan-Jaworowska, 1970: 975; *Morganucodon*: Kermack *et al.*, 1981: figs. 51A, 98). As in *Morganucodon*, the median keel does not extend into the internal nares but a cartilaginous nasal septum surely was developed. The septum is ossified in *Cynognathus* (Broili and Schröder, 1934: fig. 3) and in multituberculates and *Ornithorhynchus* (Kermack *et al.*, 1981: 60). The lateral trough in *Kayentatherium* is wider and more shallow than in *Morganucodon* and the median troughs are confluent at their anterior termini well behind the choana, different from the condition restored in *Morganucodon*. Kielan-Jaworowska (1970: 975) has interpreted the lateral troughs in multituberculates as areas for muscle attachment, specifically for M. tensor veli palatini, and the median troughs as respiratory passages. Barghusen (1986) disagrees with this restoration and regards the lateral troughs as passages for the eustachian tubes. This would be consistent with Presley and Steel's (1978: 106) suggestion that the lateral flange of the pterygoid is homologous to the hamulus pterygoidei of the mammalian ala temporalis. The configuration of this region of the palate might represent an essentially mammalian pattern.

A distinct posterolateral flange is developed along the posterior ramus of the pterygoid (fl.pt, Fig. 3). A comparable feature has not been reported previously in any non-mammalian synapsid. It possibly served as the site of origin for an equivalent of the mammalian medial (internal) pterygoideus and/or tensor tympani muscle.

Basisphenoid and parasphenoid (Bs). In absence of clear sutural delineation be-

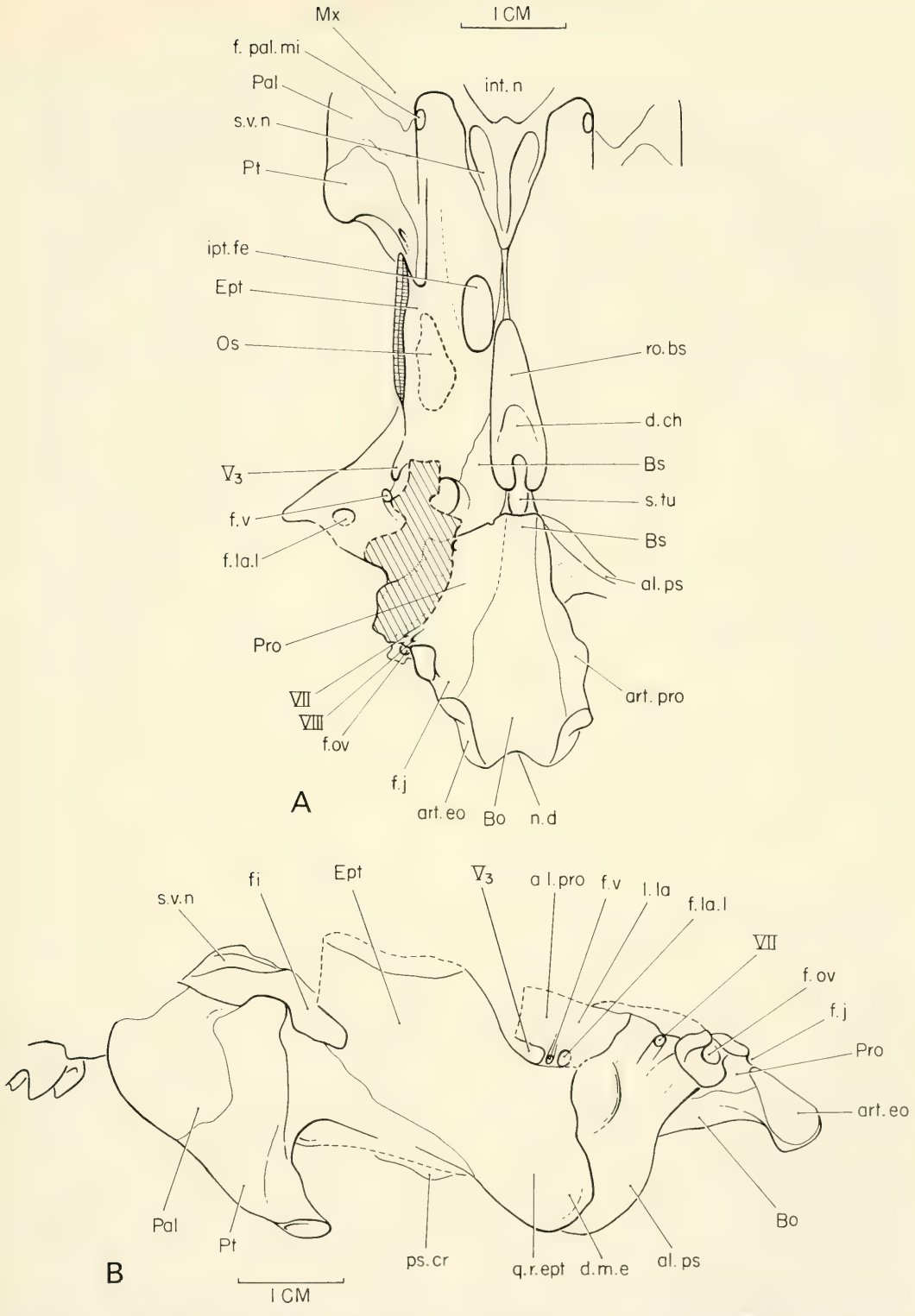


Figure 11. Incomplete basicranium of *Kayentatherium wellesi*, MCZ 8811. A) partial dorsal view. B) left lateral view. Hatching denotes broken surfaces; broken lines indicate incomplete edges.

tween the basisphenoid and parasphenoid they are described here as a single element. They, together with a possible presphenoid component, form a large median ossification that floors much of the braincase anterior to the sella turcica. This sheet-like ossification is very deep vertically, especially at the point of convergence of the parasphenoid wings (al.ps, Fig. 6). The sella turcica (s.tu, Fig. 11A) is a distinct oval depression in the dorsal face of the basisphenoid, much as in *Oligokyphus* (Kühne, 1956: pl. 5, fig. 3a), and has sharp dorsal edges except posteriorly where A. carotis interna entered the sella. Above and lateral to the pituitary fossa, a small foramen is developed on either side; it presumably marks the exit for N. abducens (VI) as in *Oligokyphus* (Kühne, 1956: 53). More lateral, a small vascular canal extends vertically down along the median wall of the cavum epiptericum. The basisphenoid forms a low median keel ventral to the sella turcica. Immediately anterior to the sella, however, it forms a very deep but delicate rostrum (ro.bs, Fig. 11A), comparable to spur-like features in this position in cf. *Scalenodon* (Parrington, 1946: fig. 7B, "B PR") and in *Bienotherium* (Hopson, 1964: fig. 3) and to Hahn's "tuberculum sellae" in the paulchoffatiid multituberculate *Pseudobolodon* (Hahn, 1981: 235). The posterodorsal portion of this rostrum forms an expanded, transversely concave surface (d.ch, Fig. 11A), possibly for chiasma n. optici (Stadtmüller, 1936: 912) and comparable to a depression on the tuberculum sellae in *Pseudobolodon* (Hahn, 1981: fig. 4, "foh"). The rostrum is anteriorly continuous with the large orbitosphenoids (MCZ 8812).

In immature specimens of *Kayentatherium* (MCZ 8811 and USNM 317203), a large oval opening (ipt.fe, Figs. 6, 11A) is developed in the floor of the cavum cranii anterior to the basipterygoid process. Its margins are largely defined by the posterior portion of the pterygoid. True interpterygoid vacuities were previously known in the much more primitive *Procynosuchus* (Kemp, 1979: fig. 12) and, among advanced synapsids, in the tritheledontid *Chalimia* (Bonaparte, 1980: fig. 4). Small openings in a similar position have been noted in a juvenile of *Thrinaxodon* (Estes, 1961: fig. 2, "iv"), and their presence in MCZ 8811 and USNM 317203 appears to attest further to the immaturity of these specimens. These features may be homologous to the foramina labelled "vid.c." in *Luangwa* by Kemp (1980: fig. 9A) and "FOR" in *Exaeretodon* by Bonaparte (1962: fig. 4) and mark the reentry into the skull of the ramus palatinus of N. facialis (Parrington, 1946: 184).

The cultriform process of the parasphenoid is very narrow and has a deep ventral keel (Fig. 11B) along its entire length. The keel has an arcuate ventral margin and reaches its greatest depth between the interpterygoid vacuities in MCZ 8811. The parasphenoids form large posterolateral wings or alae, which enclose a broad and transversely concave posteromedian surface between them (al.ps). The considerable development of the alae is presumably related to the substantial hypaxial flexor musculature for the large head. The wings also provide a partial floor to the cavum epiptericum.

Orbitosphenoid (Os). The homology of this large bone (MCZ 8812; Fig. 3) with the orbitosphenoid of therian mammals is uncertain. As in monotremes (Kuhn, 1971: 86), the element in question is not suturally separated from the remainder of the sphenethmoid complex but it can be identified on the basis of topographical criteria. It is called orbitosphenoid here, following Bonaparte (1962: 159) and Hopson (1964: 14). In the Anomodontia, a similar extension of the sphenethmoid forms part of the lateral wall of the braincase (e.g., *Lystrosaurus*; Cluver, 1971: fig. 2). In both Tritylodontidae (MCZ 8812) and Tritheledontidae (Crompton, 1958: 195), the orbitosphenoid contacts the prootic posteriorly at the dorsal end of the pila antotica.

The posterior part of the orbitosphe-

noid lies well medial to the epipterygoid. Anteriorly, its lateral wings contact the orbital portion of the palatine anteroventrally and the frontal anteriorly. Each lateral wing is rather thin. Anterodorsally, it forms the posterior margin of a large foramen orbitonasale (f.o-n, Fig. 3; for the passage of both N. and A. ethmoidalis), similar to that in *Exaeretodon* (Bonaparte, 1962: fig. 5, "FOR.ETH?") and in *Tachyglossus* (Kuhn, 1971: fig. 37). N. opticus (II) emerged through a short canal between the anterior margin of the epipterygoid and the orbitosphenoid above the fissura orbitalis (Fig. 3). The lateral wings of the orbitosphenoid converge on each other posteriorly and become continuous with the sphenethmoid complex. The resulting structure, an extensive ossified septum interorbitale, is thin except dorsally where the wings form a trough. This dorsal trough presumably corresponds to the embryonic planum supraseptale and formed a floor to the anterior portion of the brain, much as in *Bienotherium* (Hopson, 1964: 14) and *Exaeretodon* (Bonaparte, 1962: 159; Bonaparte 1966: fig. 6B).

Epipterygoid (Ept). The ascending part of the epipterygoid (Figs. 3, 11B) is a wide and tall sheet of thin bone that forms a substantial portion of the secondary lateral wall of the cavum cranii. The lamina is especially expanded along its dorsal margin where it broadly overlaps the posteroventral part of the frontal and the ventrolateral portion of the parietal (MCZ 8812). The fissura orbitalis (fi) produces a fairly large emargination in the anterior border of the epipterygoid bone. A smaller incisure is made further dorsally by the foramen for N. opticus (II). The posterior edge of the ascending process forms the anteroventral margin of the foramen for V_2 and the anterior margin for the exit of V_3. The remainder of the margins of these foramina is formed by an anterior extension of the prootic.

Presley and Steel (1976) have challenged the widely accepted homology of the mammalian ala temporalis with the ascending process of the epipterygoid in advanced non-mammalian synapsids. They noted that the former separates the exits for the mandibular and maxillary branches of N. trigeminus whereas in the latter both rami emerge behind the processus ascendens. Presley and Steel (1976: 453) claimed the presence of a short process from the epipterygoid participating in the formation of a bony partition between the two trigeminal foramina in a specimen of "*Trirachodon*" (=cf. *Scalenodon*), which is housed in the University Museum of Zoology, Cambridge University. They regarded this process as the precursor of the mammalian ala temporalis. I found no indication of such a process in the new material of *Kayentatherium* or in their specimen; in all these examples, the epipterygoid forms the anterior margins of the trigeminal foramina. The mammalian alisphenoid possibly includes the processus ascendens of non-mammalian synapsids *and* part of the anterior lamina of the periotic. This hypothesis is fully consistent with various embryological demonstrations of more than one center of development in the mammalian alisphenoid (Presley, personal communication).

Below the orbital fissure, a slender process of the epipterygoid extends medially to the lateral flange of the pterygoid. The deep, flange-like posterior process of the epipterygoid (q.r.ept, Fig. 11B), homologous to the quadrate ramus in *Thrinaxodon*, sharply turns posterolaterally behind the sutural contact with the basisphenoid at an angle of about 45° from the sagittal plane (Fig. 6), much as in *Bienotherium* (Hopson, 1964: fig. 2). The rounded posterior margin of each posterior flange is turned outward and forms a somewhat thickened edge. A distinct depression (d.m.e, Fig. 11B) is developed near the posterolateral margin of the flange. Much of the flange lies well below the level of the space occupied by the brain. The posterior process did not contact the quadrate

and lies ventral and medial to the crista parotica (Fig. 3) without contacting it. The same condition is developed in both *Bienotherium* (Hopson, 1964: 7) and *Tritylodon* (SAM K405). The epipterygoid has a distinct sutural contact medially with the basipterygoid process of the basisphenoid (Fig. 11A).

Periotic. The opisthotic and prootic are fused to form a periotic as in *Oligokyphus* (Kühne, 1956: 48).

The prootic (Pro, Fig. 3) has a relatively large lateral exposure in comparison to more primitive forms such as *Thrinaxodon* (Hopson, 1964: fig. 1) and *Cynognathus* (Broili and Schröder, 1934: fig. 4). Anteriorly, a small foramen for the exit of ramus maxillaris (V_2) and, more ventrally, a large opening for the passage of ramus mandibularis (V_3) of N. trigeminus are situated on the suture with the epipterygoid (q.v.). A similar arrangement was illustrated by Parrington (1946: fig. 7A) in cf. *Scalenodon* and by Broom (1911: pl. 46, fig. 1) in *Cynognathus* (but see Broili and Schröder, 1934: fig. 4). The anterodorsal portion of the prootic forms a thin sheet of bone (anterior lamina of authors; a.l.pro, Fig. 11B), which overlaps the ventrolateral part of the parietal posteriorly. It contacts the ascending process of the epipterygoid anteriorly. An important difference between *Kayentatherium* (MCZ 8811 and 8812) and *Bienotherium* (Hopson, 1964: 10) is the absence of the "ventrolateral flange" below the exit for V_3 in the former.

Behind the exit for V_3 the prootic is drawn out into a prominent, laterally and slightly posteriorly directed flange (l.la, Figs. 2, 3, 11B). This structure is almost vertically positioned and is identical with the posteroventral flange in other Tritylodontidae (Hopson, 1964: 12; lateral lamina of Kühne, 1956). It is pierced by a large foramen (f.la.l; Fig. 11), presumably the passage of V. capitis lateralis. A second, slightly smaller foramen is situated just lateral to the latter in MCZ 8812, much as in *Tritylodon* (SAM K405). The posteroventral flange enclosed the pterygoparoccipital foramen anteriorly but apparently not laterally. In MCZ 8811, a small foramen is located in the prootic just behind the medial recess for the semilunar ganglion (f.v, Fig. 11); a remark by Kermack *et al.* (1981: 92) to the contrary notwithstanding, it probably represents the exit for V. cerebralis media, which drains into V. capitis lateralis. A similar foramen has been observed in *Bienotherium* (Hopson, 1964: fig. 2) but MCZ 8812 lacks this feature and the vein presumably exited through the foramen for V_3.

The large cavum epiptericum lies medial to both the anterior portion of the prootic and the epipterygoid as in *Bienotherium* (Hopson, 1964: 14). Except for partial flooring by the parasphenoid alae, no floor is developed to the cavum, unlike the condition in *Morganucodon* and *Sinoconodon* (Crompton and Sun, 1985: 109). The semilunar ganglion was housed in a fairly deep recess in the medial face of the prootic (MCZ 8811), which is bordered behind by a distinct semicircular rim. An enormous space ventrolateral to the brain is enclosed laterally by the quadrate ramus of the epipterygoid and the prootic and medially by the para-basisphenoid complex (Fig. 6). Posteriorly, this space served as a passage to a wide eustachian tube, as interpreted by Watson (1942: 104), and A. carotis interna and N. facialis traversed it. The pila antotica is ossified as a short process anteromedial to the hollow for the semilunar ganglion (MCZ 8812), much as in *Bienotherium* (Hopson, 1964: fig. 3, "P A"). As in *Bienotherium* (Hopson, 1964: 14), the prootic participates with the basisphenoid in the formation of the dorsum sellae (Fig. 11A).

The paroccipital process is short but massive. As in other Tritylodontidae (Ginsburg, 1962: fig. 11; Crompton, 1964: fig. 8; SAM K 405), it is much expanded anteroposteriorly and is divided by a ventral continuation of the squamosal sulcus into two distinct projections (Fig. 3). The anteroventral projection (a.p.pr) is bul-

bous and massive. Its lateral surface is devoid of perichondral bone. Hopson (1966: 443) and Kuhn (1971: 98) homologized this projection with the crista parotica in monotremes. Furthermore, Hopson noted a distinctly posteromedially curved process on the crista parotica in *Bienotherium* that appears to correspond to the hyoid process on the monotreme crista parotica. This feature is beautifully preserved in MCZ 8812 (p.hy.c, Fig. 3) and its distal extremity shows a distinct pit. The attachment of the stylohyal to the crista parotica in both monotremes and therians lies posterior to the external auditory meatus (Presley, personal communication). This was also the case in *Kayentatherium* (shy, Fig. 22) if the course of the external auditory meatus has been correctly restored. The posterodorsal projection of the paroccipital process also lacks a cover of perichondral bone laterally (p.p.pr, Fig. 3). It may be compared to the mammalian mastoid process and possibly served as the site of origin of a jaw-opening muscle. A shallow but extensive depression is located on the ventral aspect of the paroccipital process posteromedial to the crista parotica. Similar features in *Oligokyphus* (Kühne, 1956: 49) and *Tritylodon* (Ginsburg, 1962: fig. 11, "m.st.") have been interpreted by these authors as containing a stapedius muscle. It is equally plausible that this depression was occupied by M. levator hyoidei as in monotremes (Kermack *et al.*, 1981: 98).

The fenestra ovalis (f.ov) forms a deep pit, which is surrounded by a distinct bony rim (MCZ 8811; Fig. 11B) as in *Oligokyphus* (Kühne, 1956: fig. 13, "s"). The thick ventral portion of this rim was interpreted by Kühne to have been in contact with the stapedial foot-plate. Three foramina can be traced within the internal auditory meatus in MCZ 8811 and MCZ 8812. The anterior canal was for N. facialis (VII); a small foramen in its floor, right at the medial entrance into the meatus, opens into a canal that exits anteroventral to the fenestra ovalis in a foramen pro N. faciali (VII, Fig. 11). The posterior canal is large and contained the ramus cochlearis of N. acusticus (VIII). The dorsal canal presumably carried the vestibular branch of VIII. An anteroposteriorly elongate foramen jugulare (for V. jugularis interna) is situated behind the fenestra ovalis.

The pterygo-paroccipital foramen (f.pt-p, Fig. 2) is large. V. capitis posterior, which drains the occipital musculature, probably passed forward through the posttemporal fossa to join V. capitis lateralis to form a common trunk. This trunk continued through the pterygo-paroccipital foramen to drain into V. jugularis interna. It is bordered by the posterolateral flange of the prootic anteriorly and by the crista parotica and squamosal posteriorly and medially. It is connected to the posttemporal foramen (f.p.t, Fig. 2) behind by a broad and shallow sulcus. A vascular canal enters the posttemporal fossa anteromedially (MCZ 8842); an identical canal in *Bienotherium* has been equated with the open groove ("sinus canal") in *Diademodon* (Watson, 1911) and other forms by Hopson (1964: 8). In some more primitive Tritylodontoidea (cf. *Scalenodon*; Parrington, 1946: fig. 7) the canal is already partially covered laterally by the prootic. Most authors believed that this canal contained an extracranial vein draining the orbital region; most recently, this vessel was homologized with V. temporo-orbitalis (Shindo, 1915) by Kermack *et al.* (1981: 91). But V. temporo-orbitalis extends *lateral* to the jaw musculature in embryonic *Lacerta* (Shindo, 1915: 412 and figs. 21–22) and, therefore, cannot be homologized with the feature in question in advanced synapsids. In *Oligokyphus* (Kühne, 1956: 49), a large foramen is developed in the fossa subarcuata, opening into a canal on the outside, strikingly similar to the condition in certain Multituberculata such as *Catopsalis* (Kielan-Jaworowska *et al.*, in press). No such foramen is developed in the relatively shallow fossa in *Kayentatherium* (MCZ 8812). Kielan-Jaworowska *et al.* (1984 and

in press) have argued that these canals or grooves contained arteries entering the region through the posttemporal fossa, perhaps similar to A. diploetica magna in *Tachyglossus*. While the evidence remains inconclusive, the possibility of primarily arterial affinities for the canal in tritylodontids discussed above seriously remains to be considered.

Just dorsal to the fossa subarcuata in *Oligokyphus*, a depression, misidentified as for the "lateral lobe of the cerebellum" by Kühne and Crompton, may be related to a venous sinus, possibly homologous to the mammalian sinus transversus (cf. *Ptilodus*; Simpson, 1937: fig. 8B, "S.T.S.").

Basioccipital (Bo). The basioccipital (Fig. 11) forms the posterior portion of the floor to the cavum cranii. Along its posterior margin between the occipital condyles it forms a shallow notch for the reception of the large dens (n.d, Fig. 11A). The dorsal surface of the basioccipital is transversely concave. Its ventral aspect bears a distinct, rounded median ridge, which separates the depressions for insertion of M. rectus capitis anterior (seu ventralis; d.m.r, Fig. 6). Extensive lateral facets for the exoccipitals are developed (MCZ 8811; art.eo, Fig. 11). The basioccipital becomes thicker anteriorly toward its sutural contact with the basisphenoid.

Exoccipital. The exoccipitals exclusively form the occipital condyles and presumably the lateral margins of the foramen magnum. Each is penetrated by a single, obliquely anteroventrally extending canal for N. hypoglossus (XII; MCZ 8839). Its dorsal extent cannot be determined on the available material.

Tabular. The tabular forms the dorsolateral portion of the occipital plate, including much of the lambdoidal crest, and the dorsal margin of the posttemporal foramen on the occiput. Its posteroventral portion is clearly separated from the posterior paroccipital process by a groove on the occipital plate.

Interparietal and supraoccipital. Inadequate preservation of the available specimens makes tracing of the sutural outlines of both bones impossible. A distinct median ridge in MCZ 8812, flanked by a depression on either side, presumably served as attachment for a well-developed ligamentum nuchae.

LOWER JAW

Dentary (D). The dentary is the largest bone of the mandible and has a very tall coronoid process (co.p, Figs. 12, 13). The ventral margin is gently sigmoid behind the pronounced posteroventral part of the symphysis. As in *Bienotherium* (Hopson, 1966: fig. 3F) the mandibular symphysis (sy.m, Fig. 13B) is relatively shorter than that of *Oligokyphus* (Kühne, 1956: fig. 7B), and the incisor is less procumbent. The symphysis was not fused, and the symphyseal facet extends posteriorly to the level of the first lower postcanine tooth. A distinct but small angular process (an.p) is developed on the posteroventral angle of the dentary in MCZ 8811 (Fig. 13) but not in the very large specimen MCZ 8812 (Fig. 12). *Dinnebitodon* also has a small angular process (MNA V3222). Elsewhere, *Bienotherium* appears to have a prominent process on the angle (Young, 1947: fig. 5) but in *Oligokyphus* the posteroventral corner of the dentary forms almost a right angle (Kühne, 1956: fig. 7; Sues, 1985b: fig. 4A). Just above the angle there is a smoothly curving notch in the posterior margin of the dentary. The angle of the dentary bears distinct striations on the lateral aspect in MCZ 8812 (i.m, Fig. 12), here interpreted as the site of insertion for the superficial masseter muscle. The medial surface of the angle is flat and has a rough surface texture (MCZ 8811).

The coronoid process is very high, with a nearly vertical anterior margin in MCZ 8812 (Fig. 12) and a rounded dorsal border. In MCZ 8811 (Fig. 13), an immature specimen, the angle enclosed between a tangent to the anterior margin and the long axis of the dentary is 55°. The ascending ramus apparently became more

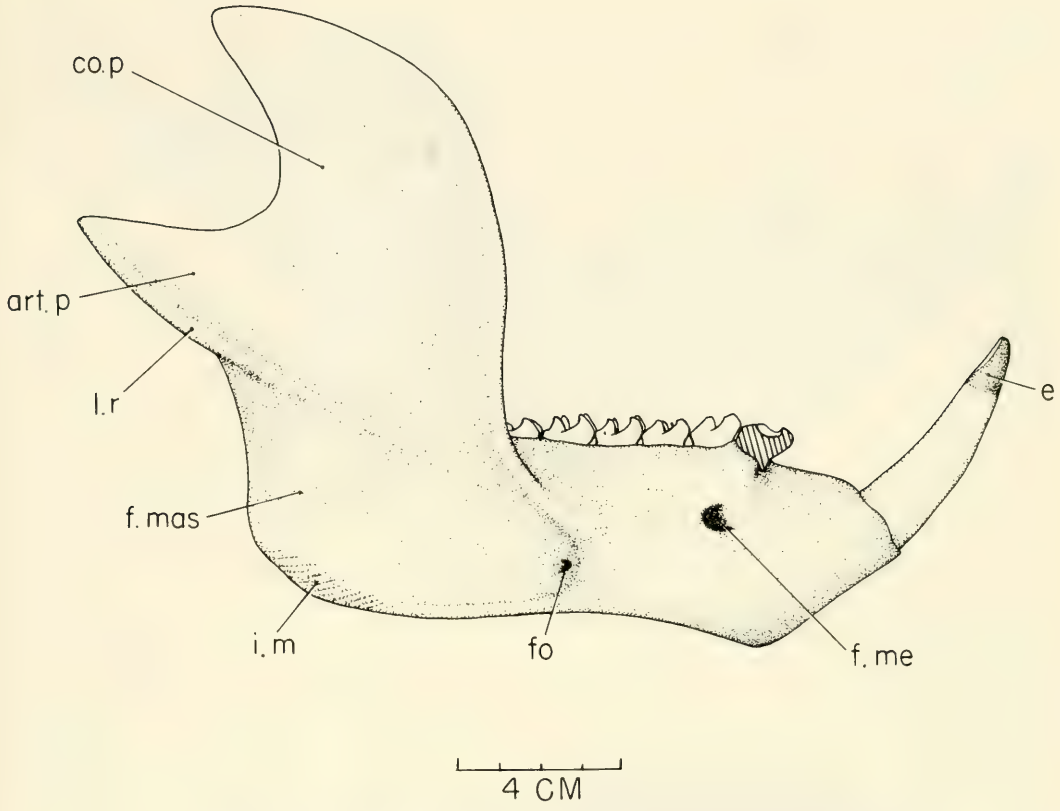


Figure 12. Right dentary of *Kayentatherium wellesi*, MCZ 8812. Lateral view.

upright during ontogeny, much as in mammals (e.g., *Homo*; Enlow, 1982: 148 and fig. 3–101). The anterior margin of the coronoid process forms a rounded ridge laterally, merging with the lateral surface of the tooth-bearing ramus of the dentary anteroventrally. The coronoid process is recurved posterodorsally to form a prominent hook (MCZ 8812), much as in *Tritylodon* (SAM K405) and "*Tritylodontoideus*" (Fourie, 1968: fig. 3A, "C.P."). The medial surface of the anteroventral portion of the ascending process is thickened to form a triangular buttress against which the coronoid bone is apposed (co.b, Fig. 14).

A well-developed masseteric fossa (f.mas) is developed on the posterolateral aspect of the dentary (Figs. 12, 13A). It is divided by a rounded lateral ridge (l.r) that extends from about the center of the fossa to the articular process of the dentary where it becomes a narrow, flange-like projection. The ventral margin of the dentary is broadly rounded and wide in the region of the symphysis, becoming increasingly more narrow and less rounded posteriorly. A small foramen is occasionally developed near the anteroventral terminus of the masseteric fossa (MCZ 8812). A low lateral ridge is developed just anterior to the anterior end of the fossa in *Dinnebitodon*; it appears to be closely similar to a very distinct lateral shelf in this position on the dentary of *Bocatherium* (Clark and Hopson, 1985: fig. 1). A mental foramen (f.me) for exit of ramus mentalis of N. alveolaris inferior is situ-

ated below the anterior margin of the first lower postcanine tooth.

A single enlarged incisor is held in the collar-like alveolar process of the dentary in most specimens. It projects forward and upward. In one small, presumably juvenile specimen of *Dinnebitodon*, MCZ 8831, the base of a second, much smaller incisor is present. Older individuals of *Bienotherium* have also only a single lower incisor (Young, 1947: 451; Hopson, personal communication) whereas *Oligokyphus* may have up to three lower incisors (Kühne, 1956: fig. 7). A ridge (r.d) is developed between the incisor and the first lower postcanine tooth on the alveolar margin of the dentary.

The two mandibular rami diverge little posteriorly. As in *Oligokyphus*, the highest degree of divergence appears to occur in very small specimens such as MCZ 8839.

Corresponding to the lateral ridge on the coronoid process, there is a much more pronounced flange-like median ridge (m.r, Fig. 13B). As a result the articular process of the dentary (art.p) forms an inverted T in transverse section. The median ridge overhangs a wide, smoothly concave groove ("Meckelian sulcus" of Simpson; p.d.tr) for the reception of the postdentary bones. This sulcus extends from the mandibular foramen to the tapering posterior end of the articular process. The ventral limit to the groove is formed by an edge that extends from the mandibular foramen to the notch in the posterior margin of the dentary above the angle. The foramen mandibulare posterius (f.d) for A. and N. alveolaris inferior is large. Just anterior to the foramen, the internal groove (i.gr) commences, extending to the posterior end of the symphysis. This sulcus probably contained a persistent Meckelian cartilage, along with mylohyoid branches of A. and N. alveolaris inferior. It was at least partially covered by the splenial bone in life although the splenial is not preserved in any specimen. A division in the wall of the groove along much of its course can occasionally be observed, providing further evidence for its double function as sulcus primordialis and sulcus mylohyoideus (Krebs, 1971: 93). On a few dentaries a distinct but short groove is located immediately behind the symphysis near the ventral margin of the dentary; it is apparently continuous with the internal groove posteriorly.

The lower postcanine tooth row twists behind the symphysis so that the more anterior teeth point laterally (at about 10°) and the more posterior teeth (especially the newly erupted ones) point medially (at about 20°) in MCZ 8811. The crowns of the more anterior postcanines also point increasingly forward. The twisting of the tooth row is particularly pronounced in immature specimens such as MCZ 8811. The dentary is recessed lateral to the tooth row more posteriorly.

Coronoid (Co). The coronoid (Fig. 13B) is a more or less triangular bone located on the raised boss (co.b, Fig. 14B) on the medial aspect of the coronoid process of the dentary. Anteroventrally, it overlaps the medially expanded portion of the dentary that holds the posterior postcanine teeth. The lower half of the coronoid encloses a hollow (c.r.t) containing unerupted replacement teeth, much as in *Bienotherium* (Young, 1947: fig. 5). The anterior face of the coronoid is nearly vertical but its base is anteroventrally inclined. Two small foramina pierce the anterior aspect of the bone just above the level of the tooth row in MCZ 8811. The expanded base of the coronoid has a long posteroventral process that contacts the prearticular below and consists of very thin bone. It overlies the median ridge above the postdentary trough. The coronoid is especially thick posterodorsally. Its dorsal portion appears swollen and bears the same vermiculate texture that is developed on the pterygoid flange. The posterior face of the coronoid is deeply excavated in MCZ 8811 (Fig. 13B). The dorsal edge is rounded. When the mandible is occluded with the skull, the dorsomedial surface of the coronoid bone contacts the dorsolateral as-

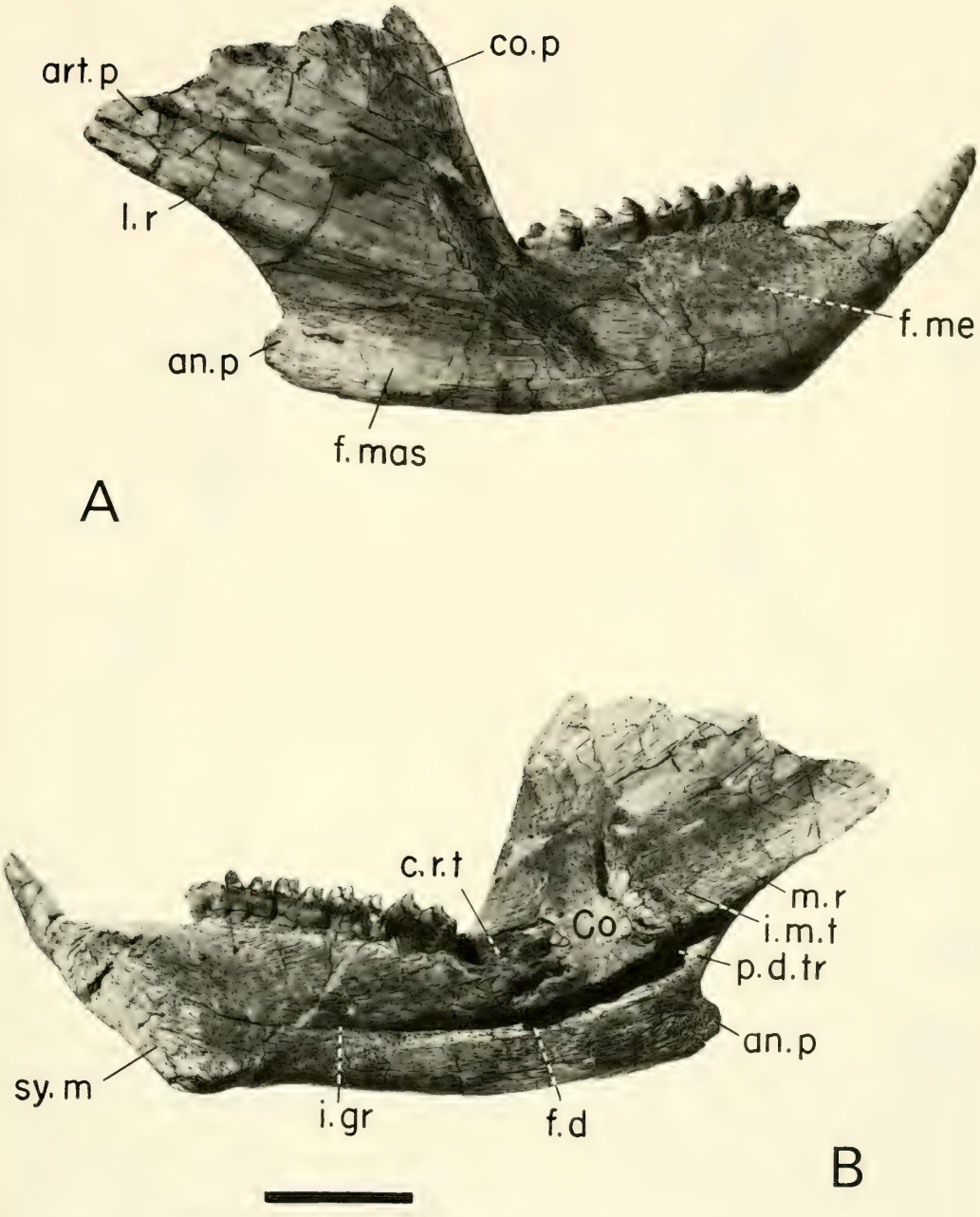


Figure 13. Right dentary of *Kayentatherium wellesi*, MCZ 8811. A) lateral view. B) medial view. *Scale bar*. 2 cm.

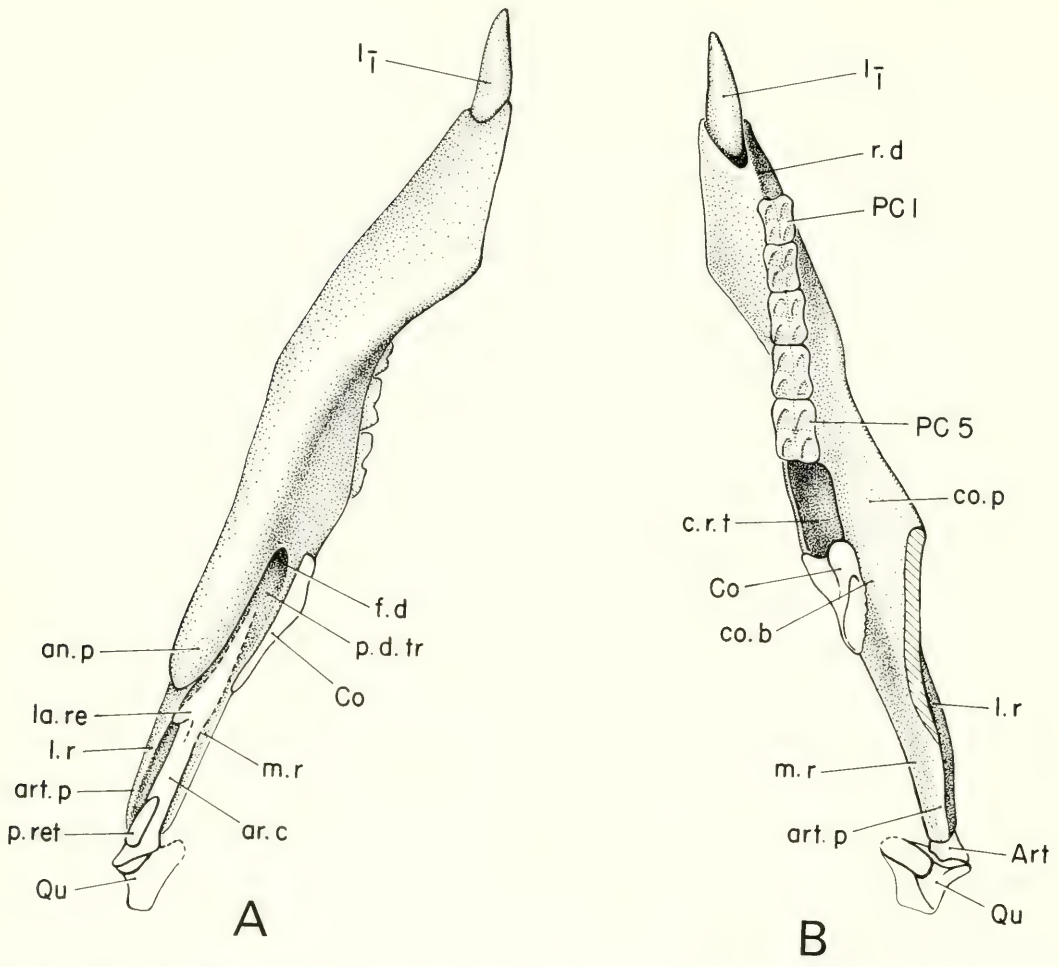


Figure 14. Lower jaw of *Kayentatherium wellesi*, MCZ 8811. Reconstruction in (A) ventral and (B) dorsal views. Hatching denotes broken coronoid process.

pect of the lateral flange of the pterygoid. This would have suppressed any significant transverse movements of the mandible (Watson, 1942: 108).

Kühne (1956: 34) claimed that *Oligokyphus* did not have a coronoid bone but the raised triangular contact of that element with the dentary is readily apparent and the coronoid has obviously been lost post-mortem. The mandible of the holotype of *Bienotherium yunnanense* Young, 1940 has this bone developed much as in *Kayentatherium* (Young, 1947: fig. 5).

Articular and surangular (Art). The articular complex (Figs. 14–16) is composed of the indistinguishably fused articular and surangular. The anterior portion of this complex forms a slender, tapering rod (ar.c) that was closely applied to the walls of the sulcus on the posteromedial aspect of the dentary. The lateral aspect of the articular rod is divided by a ridge into two surfaces, which are inclined on each other; the dorsolateral field contacts the dentary and the ventrolateral field the angular (MCZ 8811). A shallow depression extends along the medial surface.

The most prominent feature of the robust posterior portion of the articular complex is the large retroarticular process

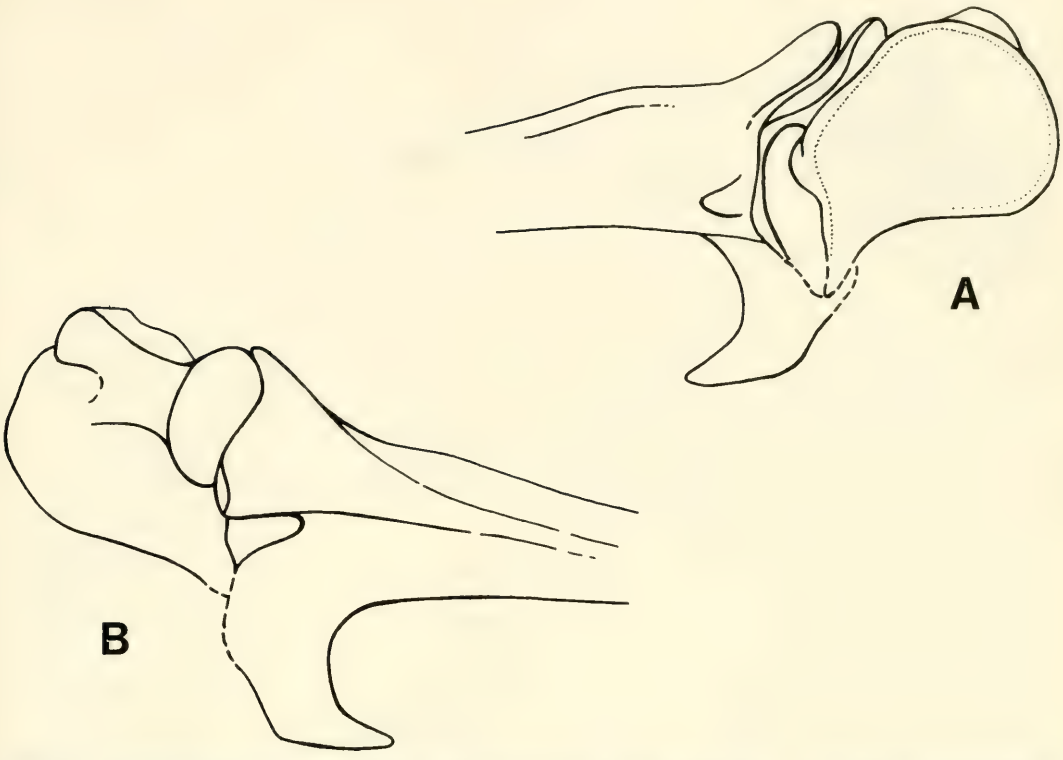


Figure 15. Articulated right quadrate and articular of *Kayentatherium wellesi*, MCZ 8811. A) medial view. B) lateral view. Based on camera lucida sketches.

(p.ret, Fig. 16) with a forwardly directed "hook," which is closely similar to the manubrium mallei in monotremes (Hopson, 1966: fig. 8; Kuhn, 1971: fig. 4). The hook has a relatively thick posterior rim, apparently corresponding to the orbicular apophysis on the monotreme malleus (Fleischer, 1973: fig. 1), and is filled out by thin bone. The lateral surface faces anterolaterally and is concave dorsoventrally. The distal extremity of the retroarticular process is expanded and its ventral face is flat or gently concave. A foramen (fo.ch.t), probably for the chorda tympani (VII), is developed on the medial aspect of the base of the retroarticular process just below the articular facet for the quadrate trochlea. The chorda tympani would have had the same topographical position as in embryonic mammals (Fig. 23A).

The articular facet (art.f) for the quadrate trochlea forms a deeply concave notch, which is partitioned into a small lateral and a larger medial facet. It is overhung by a distinct dorsal lip except for its medial portion. The notch is delimited ventrally by a pronounced horizontal ridge (when viewed from behind). This ridge appears to be drawn out into an acute posterior projection (d.p) in lateral view, much as in *Oligokyphus* (Kühne, 1956: fig. 8). The articular notch is open medially. The medial facet is more concave than the lateral one. The transverse axis of the articular notch is strongly inclined anteromedially (about 30° or 150°) relative to the long axis of the articular rod (MCZ 8811). A blunt projection located just anteroventral to the articular notch (p.mus) is identical with a tubercle in *Oligokyphus* (Kühne, 1956: fig. 8B, "P.i.") and a rugosity in the same position on the articular in *Morganucodon* (Kermack *et al.*, 1981: fig. 88, "ten.ty.ar."). Kühne

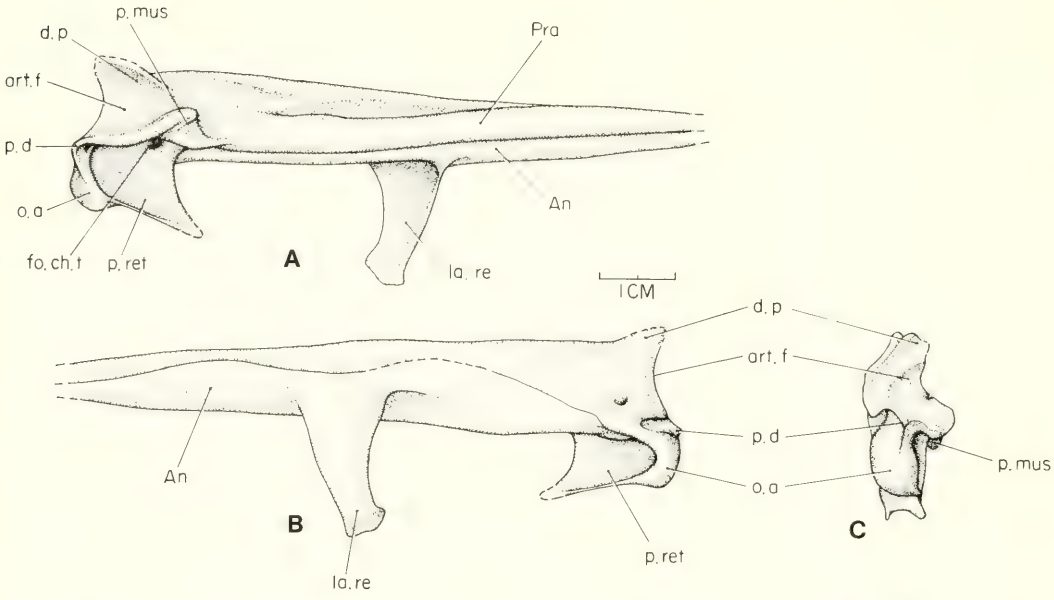


Figure 16. Left postdentary elements of *Kayentatherium wellesi*, MCZ 8812. A) medial view. B) lateral view. C) posterior view.

(1956: 38) has interpreted this feature in *Oligokyphus* as a processus muscularis for a muscle homologous to the mammalian M. tensor tympani.

The tritylodontid articular rod differs from those in *Cynognathus* (Kermack *et al.*, 1973: figs. 25, 26) and *Diademodon* (Kermack *et al.*, 1973: pl. 3, figs. F, G) especially in lacking the pronounced boss on the surangular for contact with the squamosal (incorrectly identified as the retroarticular process by Kermack *et al.*, 1973) and, furthermore, in the distinct anteromedial inclination of the articular facet.

Prearticular (Pra). The posterior sutural contact of the prearticular with the articular has been obliterated (Fig. 16A) but otherwise the bone is clearly distinct from the remainder of the articular complex. It forms a bony rod medial and slightly ventral to a median gap that is laterally enclosed by the surangular. The ventrolateral surface of the prearticular contacts the angular below.

Angular (An). The angular is situated ventral and lateral to the articular complex (Fig. 16). Its posterior portion forms a thin dorsal flange and terminates just in front of the posterior end of the retroarticular process. It is fairly thick and overlaps the lateral aspect of the articular. More anteriorly, a large reflected lamina (la.re) emerges from the ventrolateral margin of the angular rod and extends posteroventrally. It is fairly wide anteroposteriorly and only slightly curved backward. The medial surface of the broad proximal base of the lamina is excavated. Anterior to the reflected lamina the angular continues as a tapering rod (MCZ 8812, MNA V3141).

HYOID APPARATUS

A number of disarticulated elements found in the matrix behind the dentaries of MCZ 8812 are clearly referable to the hyoid apparatus. Virtually nothing has been reported in the literature about this feature in non-mammalian synapsids. A few hyoidal bones are known in dicynodonts (Cluver, 1971), and caseid pelycosaurs have a well-developed hyoid apparatus (Olson, 1968: 246; Sigogneau-Russell

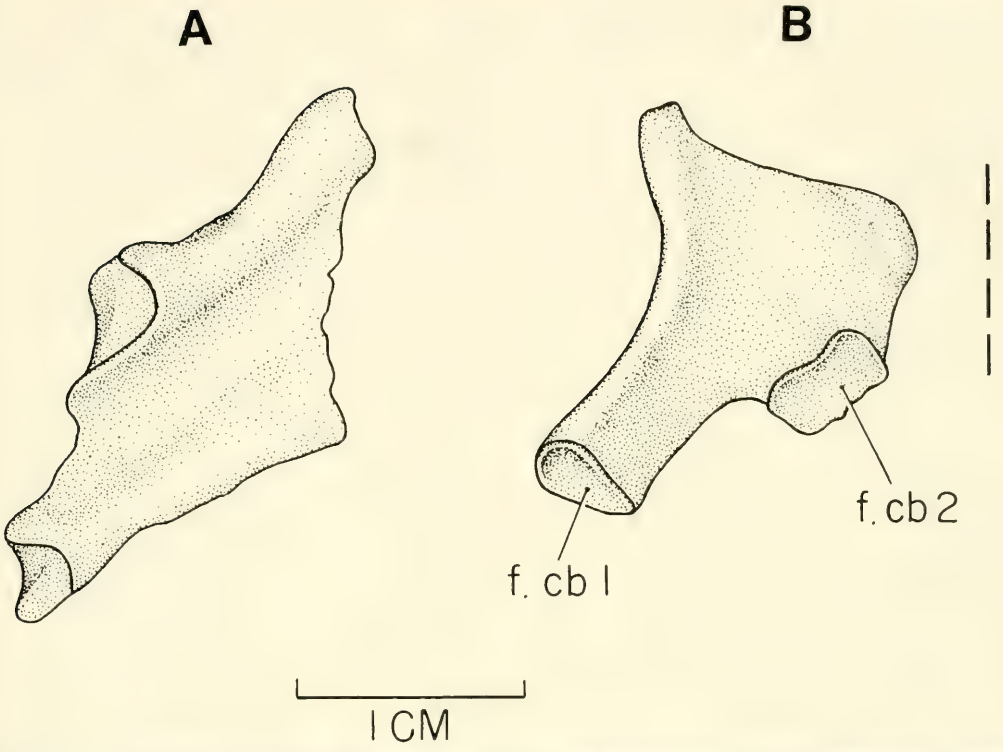


Figure 17. Hyoid elements of *Kayentatherium wellesi*, MCZ 8812. A) element from the (?) second branchial arch. B) basihyal element. Broken line indicates inferred midline.

and Russell, 1974: fig. 13). Rod-like hyoid elements are not uncommon in the galesaurids *Galesaurus* and *Thrinaxodon* (Hopson, personal communication). Identification of the slightly distorted elements in MCZ 8812 is difficult owing to the lack of extant analogues. They appear to be most similar in shape to the hyoid elements in modern turtles (Gaupp, 1905: figs. 38–40).

The first type of element, represented by bones from opposite sides, may reasonably be interpreted as a copula hyoidei. Fusion of the copulae in mammals produces the basihyal. The element (Fig. 17B) bears a prominent posterolateral process with a terminal facet (f.cb 1) and, posteromedially, a distinctly off-set second facet (f.cb 2). If it is indeed a copula, these cup-shaped facets presumably were for articulation with elements of the branchial arches 1 and 2, respectively, based on the condition in living amniotes (Gaupp, 1905). The dorsal surface of the median plate is thin and transversely concave. The bone forms a short anterolateral process, possibly for contact with a ceratohyal.

A second type of hyoidal element is an elongate, curved rod. It bears a cup-shaped facet at one end and is flattened at the other. It almost certainly represents a first ceratobranchial. There is also a shorter, straight bony rod with obliquely inclined facets at either end.

A fourth type of hyoidal element is represented by a thin rhomboidal bone. It bears two facets at one end and a smaller terminal one at the other end (Fig. 17A). One of its surfaces is distinctly concave transversely. I have not found any comparable element in another tetrapod. The bone in question may represent a segment

of the second branchial arch, homologous to the mammalian cartilago thyroidea.

DENTITION

Upper incisors. Both immature and adult specimens of *Kayentatherium* have but a single incisor in each premaxilla. This deeply rooted tooth is greatly enlarged, robust, and often recurved. It corresponds to the second upper incisor in *Dinnebitodon* and other Tritylodontidae. The enamel covering is very thin and apparently restricted to the apical portion of the crown. The long root forms an anteroposteriorly elongate oval in transverse section. A very extensive lingual wear facet was formed by contact with the buccal edge of the enlarged lower incisor. As in *Oligokyphus* (Kühne, 1956: 87), the corresponding wear on the lower incisor is extraordinarily slight. Deep oblique grooves have been cut by the lower incisors into the lingual faces of the enlarged second upper incisors in one specimen referable to *Dinnebitodon* (MCZ 8836). Although it is poorly defined in MCZ 8812, a second facet cuts away the anterior aspect of the tip of the upper incisor (Fig. 8).

Lower incisors. Typically a single enlarged lower incisor is held in each dentary in both *Dinnebitodon* and *Kayentatherium.* A second, much smaller incisor is developed only in one specimen of *Dinnebitodon* (MCZ 8831). The tusk-like lower incisor is distinctly procumbent and converges distally to meet its fellow (MCZ 8812; Fig. 8). The thin covering of enamel appears to be restricted to the anterobuccal aspect of the tip of the crown. The cutting edges are sharp. The lingual aspect of the apical region is flat and the posterior face is gently concave.

Upper postcanine teeth. The quadrangular crown of each upper cheek-tooth is divided into three anteroposterior rows of cusps by two longitudinal furrows (Figs. 18A, 19A). It is (buccolingually) wider than long. The ratio of crown width to crown length, measured on a sample of undistorted teeth, ranges from 1.04 to 1.14 and is comparable to that of most other Tritylodontidae except *Oligokyphus,* D. M. Kermack's (1982) comment to the contrary notwithstanding.

The cusps of the median row are symmetrically crescentic but those of the buccal and lingual rows are variously asymmetrically so. All crescents open forward and are buccolingually compressed. The buccal row is always shorter than the other two rows and has only two principal cusps. The medial wing on the anterior cusp extends further anteriorly than does the lateral one. The large posterior cusp, the tallest one on the entire tooth, sends a distinct posteromedial crest that extends into the groove and is more prominent than the lateral one. The median row has three cusps, which increase in size from front to back. The wings of the second cusp envelop much of the preceding cusp, which is distinctly smaller and often has an irregular, wrinkled face (MCZ 8842). Its small size led D. M. Kermack (1982) to call it an accessory cusp; however, this term is only meaningful when it is also applied to the equally small anteromedian cusp in other Tritylodontidae such as *Tritylodon.* Two crests extend from the apex of the very large posteromedian cusp to the posterior ends of the outer and inner furrows, respectively. They form posterior cingula together with ridges from the posterobuccal and posterolingual cusps, respectively.

The upper cheek-teeth of *Dinnebitodon amarali* have two asymmetrically crescentic lingual cusps, the anterior one of which is smaller than the posterior one (Sues, 1986a; Fig. 20). The posterolingual cusp sends a crest from its apex to the posterior end of the inner furrow. *Kayentatherium wellesi* has upper postcanine teeth with three lingual cusps (Fig. 18A). D. M. Kermack's (1982: 7) report of only two lingual cusps is based on the inadequately preserved and prepared type-specimen, and slight additional cleaning of the ultimate cheek-tooth in the left maxilla revealed the same configuration as described here (Sues, 1986b). The an-

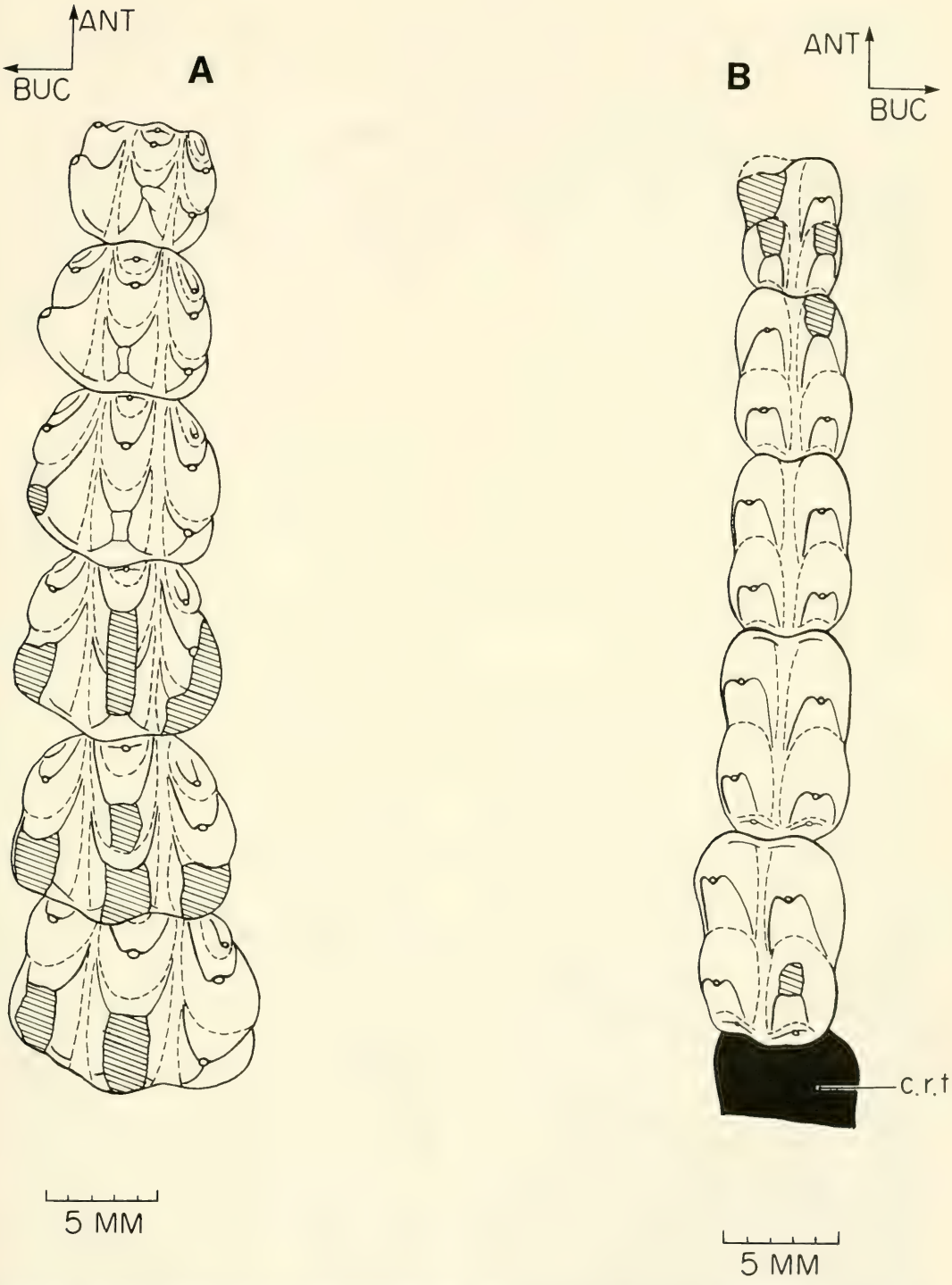


Figure 18. Postcanine dentition of *Kayentatherium wellesi*, MCZ 8811. A) right maxillary tooth row. B) right dentary tooth row. Occlusal views. Hatching denotes broken or damaged cusps.

teriormost lingual cusp is the smallest and often forms a mere ridge, extending obliquely to the anterior terminus of the inner furrow. It is completely embraced bucally by the wing of the large, distinctly asymmetrical second cusp. The latter cusp sends a posteromedial ridge to the lingual margin of the crown. The posteriormost cusp is smaller than its predecessor and its anterior face is less asymmetrical. It has a triangular outline in occlusal view and sends a distinct crest to the posterior terminus of the inner furrow.

Accessory cuspules are present on newly erupted and moderately worn teeth of both *Dinnebitodon* and *Kayentatherium*, especially near the anterior end of the buccal row of cusps (Figs. 18A, 20). These cuspules form distinct swellings on the lateral wing of the anterobuccal cusp and the medial wing of the anterolingual cusp. In some cases they are delimited by mere nicks in these crests. Butler (1939: 516) has noted similar cuspules on upper postcanine teeth in *Tritylodon*.

Two fairly slender posterior roots are arranged in a transverse row. Anteriorly, three roots are joined immediately below the level of the crown into a single transverse structure but they are distinct within the alveoli. The median root is the largest and projects well in front of the anterior margin of the extraalveolar portion of the tooth as in *Tritylodon* (Simpson, 1928: 17) and fits tightly against the posterior face of the preceding tooth.

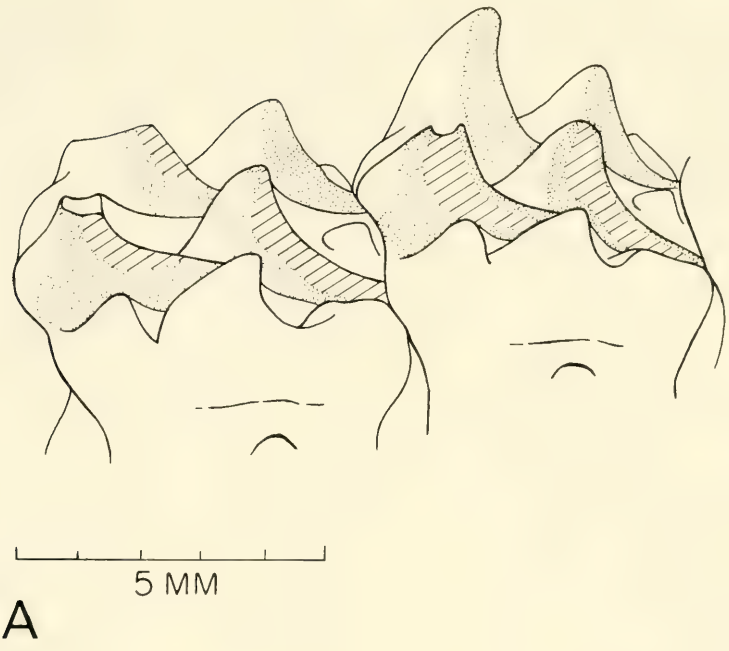
Lower postcanine teeth. The crown of each lower cheek-tooth is divided into two anteroposterior rows of cusps by a deep longitudinal groove (Figs. 18B, 19B). It is always longer than wide. Each row has two principal, symmetrically crescentic cusps. The crescents open backwards. The anterior cusp in each row is larger than the posterior one. A distinct cuspule is situated on the concave posterior face of each posterior principal cusp; these cuspules are also apparent in D. M. Kermack's illustrations (1982: figs. 8B, 9B) even though that author denies their existence. A ridge-like accessory cuspule is also developed on the convex anterior aspect of the tall anterior cusps.

The teeth have two transverse roots. The anterior root has approximately a figure-eight shape in transverse section and the posterior root is more rounded.

Ontogenetic changes in the dentition. The available sample of complete or nearly complete dentitions for both *Dinnebitodon* and *Kayentatherium* is small. Metrical comparisons of the teeth are frequently not feasible because of fracturing and distortion of the tooth crowns. Therefore, only some qualitative remarks about the mode of tooth replacement can be made at present.

Replacement of the upper incisors appears to be restricted to smaller, immature specimens in both *Kayentatherium* and *Dinnebitodon*. One specimen of the former, MCZ 8811, with an estimated skull length of about 13.5 cm (measured along ventral aspect), shows erupting teeth in crypts just posteromedial to the upper incisor (I^2r, Fig. 6). Larger individuals of this genus such as MCZ 8812, with a skull length of about 26 cm, and MNA V3141 do not display replacement of incisors. One small specimen of *Dinnebitodon* (MCZ 8830) has an erupting incisor posteromedial to the right second upper incisor whereas the larger MNA V3222, the holotype of *D. amarali*, again shows no incisor replacement.

The number of postcanine teeth increases slightly during ontogeny. Teeth are lost in front and new teeth are added at the posterior end of the tooth row as the jaw grows, much as in other Tritylodontoidea (Crompton, 1955: 649). The number of postcanine teeth in the Mid-Triassic tritylodontoid *Scalenodon* increases from five in the smallest known specimen to eleven in the largest (Crompton, 1955: fig. 12). The number of postcanines in the upper and lower jaws of *Kayentatherium* increases from five (USNM 317203 and UCMP 83671) to seven (MCZ 8812). In *Dinnebitodon*, it increases from four (MCZ 8830) to five (MNA V3222). (The discovery of further ontogenetic stages



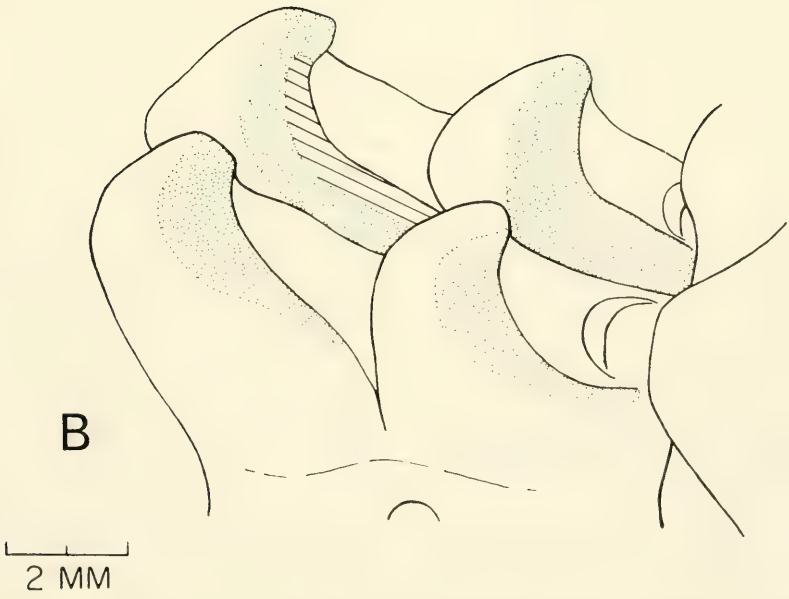


Figure 19. Wear on the right first and second upper postcanines (A) and on the right fourth lower postcanine (B) of *Kayentatherium wellesi*. Stippling indicates wear on the enamel, oblique hatching exposed dentine.

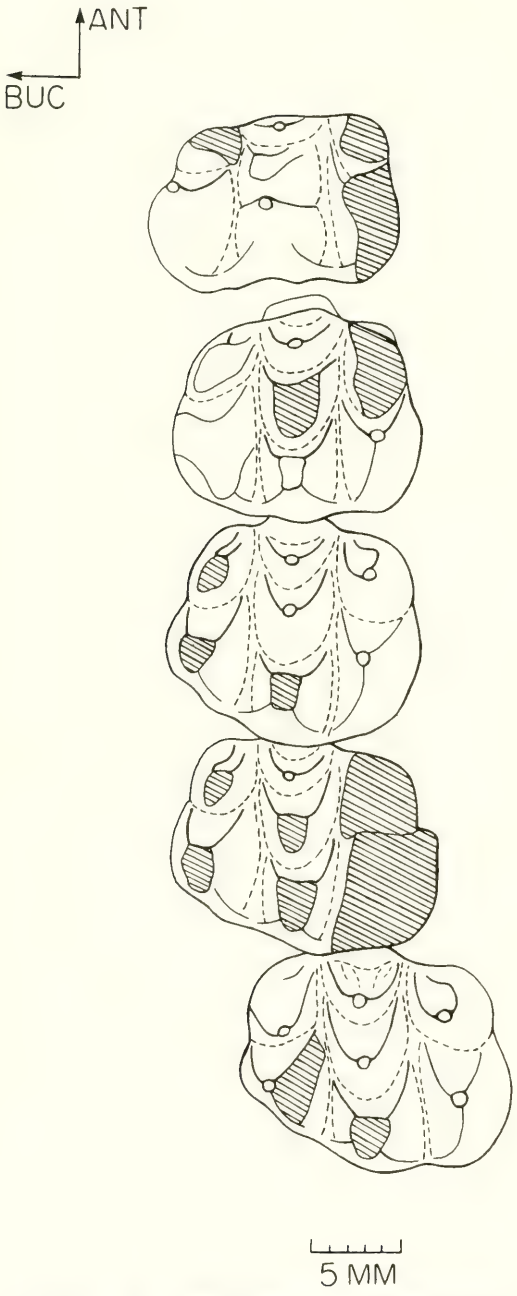


Figure 20. Right maxillary tooth row of *Dinnebitodon amarali*, MNA V3222 (holotype), in occlusal view. Hatching denotes damaged areas.

may, of course, further increase these ranges.) The posteriormost cheek-tooth is never fully erupted. The buccolingual width of the postcanine teeth increases progressively in immature specimens (MCZ 8811) but in the largest known individuals (MCZ 8812) the posterior teeth begin to decrease in width. A similar ontogenetic change has also been observed in *Bienotherium* (Young, 1947: 553) and *Oligokyphus* (Kühne, 1956: 76) as well as in more primitive Tritylodontoidea such as *Scalenodon* (Crompton, 1955: 651).

As noted previously, new teeth were added at the back of the tooth row while teeth were lost in front. Toward the anterior end of the tooth row in MCZ 8811 and 8812, the roots of the cheek-teeth become progressively more exposed through resorption of the surrounding alveolar bone. In none of the currently available specimens did I observe an empty alveolus anterior to the first functional postcanine tooth but such alveoli do occur in *Oligokyphus* (Kühne, 1956: pl. 2, fig. 3). Apparently the tooth was shed with its roots virtually intact and then the alveolus was very quickly filled with bone (Kühne, 1956: 69). This loss of anterior teeth partially contributed to an ontogenetic increase in the relative length of the diastema. New lower postcanine teeth were formed in a posterior extension of the tooth-bearing part of the dentary medial to the coronoid process (c.r.t, Fig. 13B). The bone surrounding the new teeth was thin, much as that around the replacement teeth in the maxilla. The crowns of newly erupted lower postcanines initially are inclined lingually (MCZ 8837) but they increasingly turn buccally and anteriorly further forward along the tooth row. The postcanine teeth also become more tightly appressed against one another anteriorly.

JAW MUSCULATURE

Crompton (1963) and Barghusen (1968) both have attempted detailed reconstructions of the adductor jaw musculature in advanced non-mammalian synapsids.

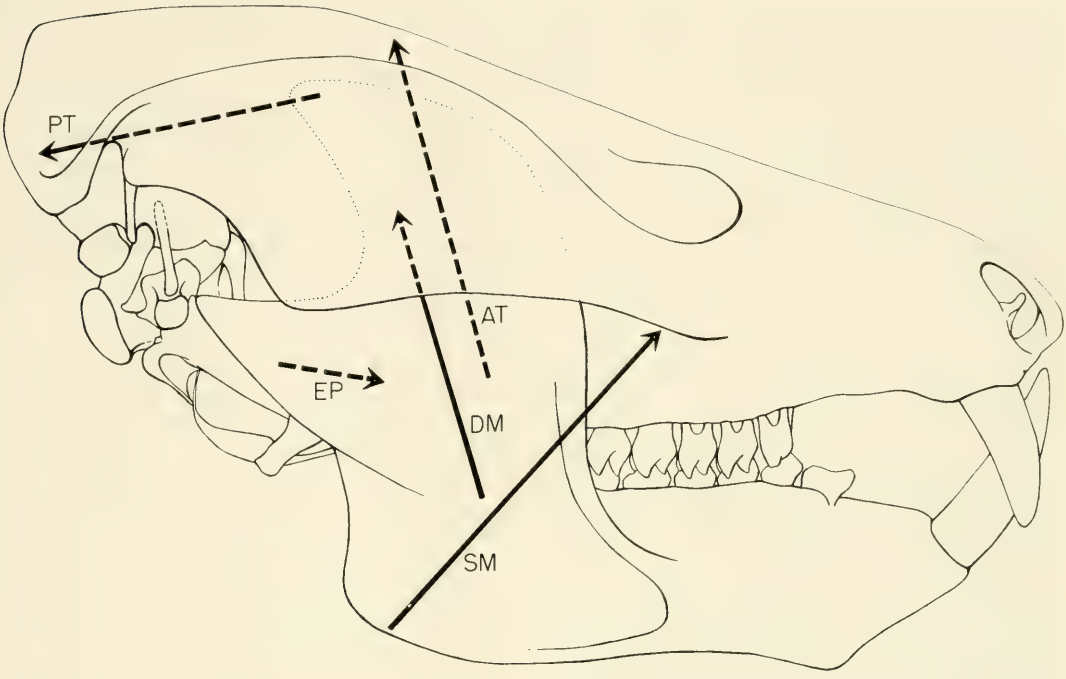


Figure 21. Diagrammatic reconstruction of the action lines for the adductor jaw muscles in *Kayentatherium wellesi*. Skull outline from MCZ 8812. Right lateral view.

Their considerations form the foundation for the following interpretation of the origins and insertions of these muscles in *Kayentatherium* (Fig. 21).

M. masseter. The masseteric fossa on the dentary is very large and is continuous over the entire lateral surface of the ascending ramus of the dentary. It is partially divided by a lateral ridge (masseteric ridge of Kühne, 1956) into a larger dorsal portion on the prominent coronoid process and a smaller ventral portion. The lateral and medial ridges on the ascending ramus have been interpreted by Crompton (1963: 719) as structural reinforcements against bending and shearing forces related to muscular contraction. A distinct change in surface topography occurs at the anterior terminus of the masseteric fossa from the floor of the fossa to the convex lateral aspect of the tooth-bearing portion of the dentary, much as on mammalian mandibles.

The deep masseter (pars profundus, DM) presumably inserted on the lateral surface of the coronoid process and formed a major component of the masseter complex. The superficial masseter (pars superficialis, SM) probably arose from the ventral aspect of the anterior root of the zygoma whereas the pars profundus arose along the medial face and the ventral margin of the deep zygoma behind the orbit. The anterior zygomatic root bears a prominent ventral ridge below the orbit. The peculiar articulation between the jugal and maxilla in the Tritylodontidae, well-illustrated in *Oligokyphus* by Kühne (1956: fig. 6), suggests considerable tensile forces produced by a posteroventrally pulling superficial masseter with a concentrated tendinous attachment. A comparable tenon-and-mortise sutural pattern has been noted in extant suids by Herring (1972: fig. 8). The long oblique suture between the jugal and squamosal may be

correlated with the action of the deep masseter extending more or less perpendicular to it. The superficial masseter inserted on the angle of the dentary as is attested by distinct striations along the ventrolateral margin of the angle in MCZ 8812 (i.m, Fig. 12). Therefore, I consider the angle of the tritylodontid dentary homologous to the angular process in therian mammals, contrary to a recent suggestion by Jenkins *et al.* (1983: 1234) that this process in non-mammalian synapsids and non-therian mammals should be called a pseudangular process, as first suggested by Patterson and Olson (1961). I believe that the "pseudangular process" in *Dinnetherium* (Jenkins *et al.*, 1983: fig. 1f–g) is actually homologous with the angle of the therian dentary and that the "angular process" is autapomorphous. It is apparent from examination of MCZ 20870, a well-preserved right dentary of *Dinnetherium*, that the "angular process" is produced by downward growth of the lateral ridge of the articular process. "Fusion" of this process with the "pseudangular process" could have produced the condition in the Multituberculata, Symmetrodonta, and Triconodonta (Simpson, 1928: figs. 9, 19) where the ventral margin of the dentary is continuous from symphysis to condyle. Pars superficialis of M. masseter in tritylodontids had an anterodorsal orientation of its fibers, presumably close to the vertical plane, whereas pars profundus (seu zygomatico-mandibularis) must have had a more posterodorsal course of its fibers.

M. temporalis. The well-developed sagittal and lambdoidal crests defining the perimeter of the temporal fossa provide suggestive evidence for the presence of a temporal aponeurosis that superficially covered the fossa (Barghusen, 1968: 27). Aside from serving as an area of origin for part of M. temporalis, this fascia probably also aided the zygomatic arch in resisting tensile forces produced by M. masseter, as has been experimentally demonstrated in mammals by Eisenberg and Brodie (1965).

As in mammals, most of the posterior temporalis fibers (PT) probably originated from the expanded posterodorsal portion of the temporal fossa, the sagittal and lambdoidal crests, and the overlying temporal fascia. The main axis of the muscle extended in a nearly horizontal plane. Its fibers must have exercised a strong posteriorly to posteromedially directed pull in the direction of the posterior V-shaped notch in the squamosal. The distinctly hook-shaped posterodorsal extremity of the coronoid process presumably formed within the joint tendinous insertion of the posterior temporalis fibers. The anterior temporalis (AT) probably originated from the well-ossified lateral wall of the braincase, especially from the extensive area behind the orbital fissure. It apparently broadly inserted on the medial aspect of the ascending ramus of the dentary above the medial ridge. A distinct pocket is formed by the excavated posterior face of the coronoid bone and the adjacent surface of the dentary (MCZ 8811; i.m.t, Fig. 13B). As restored, the fibers of the anterior temporalis have a posterodorsal orientation.

M. pterygoideus. A tubercle on the medial aspect of the articular complex anteromedial to the facet for the quadrate trochlea has been interpreted by Kühne (1956: 38) as the site of insertion for a slip of the medial (internal) pterygoideus muscle, which is presumably homologous to the mammalian M. tensor tympani. This muscle might have originated from the distinct posterolateral flange along the posterior ramus of the pterygoid. Crompton (1963: fig. 7, "i.i.p.") believed that an internal pterygoideus inserted on the medial face of the angle of the dentary. Bramble (1978: 294) has rejected that suggestion and instead suggested that a digastric-like muscle inserted at that site; I am not convinced by the arguments in support of his reconstruction.

The existence of a lateral (external) pterygoideus muscle (EP) can be hypothesized on functional grounds. None of the previously discussed jaw muscles has a sig-

nificant protractive vector component. A possible site of insertion is the smooth medial surface of the articular process of the dentary, as first indicated by Crompton (1963: fig. 7, "i.e.p.").

No direct osteological evidence exists for the presence of a depressor mandibulae muscle, which was inferred by Allin (1975). There is no trace of such a muscle during the ontogenetic development of modern mammals (Presley, 1984: 187), and M. depressor mandibulae may well prove to be a uniquely sauropsid feature. Jaw opening in both primitive and advanced synapsids could have simply been accomplished by hyoid muscles, and M. digastricus may only occur in therian mammals. Experimental evidence suggests that M. detrahens, long considered the monotreme equivalent of the therian digastric muscle, is not involved in jaw-opening in at least *Tachyglossus* (Crompton, personal communication).

FUNCTIONAL CRANIOLOGY

The masticatory apparatus of tritylodontid synapsids has undergone considerable structural modification relative to that in related non-mammalian synapsids. Recent experimental studies on mammalian mastication provide a framework within which certain features of the tritylodontid skull and dentition can be interpreted in functional terms.

Masticatory apparatus. The much enlarged incisors were clearly not adapted for gnawing or substantial incisive biting. The amount of wear, especially on the procumbent lower incisors, is surprisingly small. They probably served in seizing and holding plant material that then was torn off its substrate mainly by the power of the neck musculature, as commonly in mammalian herbivores (Weijs and Dantuma, 1975: 23). This would have limited the amount of bite force necessary and is consistent with other inferences concerning the function of the jaw joint. The well-developed tongue (judging from the hyoid skeleton and the well-developed diastema) probably aided in the gathering and, along with muscular cheeks (inferred from the arrangement of the maxillofacial foramina and from the inset tooth rows), in subsequent oral manipulation of the food. The wear facet on the anterior aspect of the tip of the enlarged upper incisor appears to be the result of contact with the substrate during rooting or other foraging activities.

During occlusion of the upper and lower postcanine teeth, the two rows of lower cusps fit between the three rows of upper cusps. Wear facets are developed on the sides of all cusps (Fig. 19) except for the buccal sides of the buccal cusps and the lingual sides of the lingual cusps on the upper teeth. These attritional facets are oriented nearly vertically and have a polished appearance. Examination at higher magnification, however, reveals the presence of parallel sets of anteroposteriorly extending microstriae, which indicate unidirectional, horizontal jaw movements. The anterior crests of the upper cusps and the posterior crests of the lower cusps can be viewed as a multiple cutting mechanism (Crompton, 1972: 61). In rodents such as *Rattus* the mandible is drawn forward during mastication; the crests on the upper molars are concave posteriorly and those on the lower teeth concave anteriorly (Rensberger, 1973: 522). As the reciprocally concave leading cutting edges meet, they enclose an ovoid space, the size of which progressively decreases during dynamic occlusion. This reversal of curvature in occluding teeth limits the area of tooth-to-tooth contact and maximizes occlusal pressure at the contacts at any given instant in time. Because the curves are usually concave in the direction of relative motion a posteriorly directed movement of the mandible can be inferred for tritylodontids, much as in multituberculates (Krause, 1982: 273). During dynamic occlusion, a lower tooth initially makes contact with an upper tooth one position further anteriorly and then, during mandibular retraction, the lower tooth comes

into occlusal contact with a second upper tooth (Crompton, 1972: fig. 13L). Because of the complex nature of the occlusal plane, produced by differences in axial tilting of the individual teeth along the jaws (see above), the postcanine teeth did not occlude simultaneously. This would have increased the bite force across individual teeth as they sequentially came into occlusion. Significant transverse movements of the mandible would have been suppressed by the occlusal relationships of the greatly enlarged incisors and of the postcanine teeth as well as by the contact with the robust lateral flanges of the pterygoid. The commonly observed apical pitting on the cusps can be related to the initial puncture-crushing action when the food bolus was crushed between the tips of the opposing teeth as the lower teeth moved upward. This wear quickly perforated the enamel. Relatively more rapidly wearing dentine was exposed (Fig. 19A), and these "windows" in the apical enamel quickly spread along the crests with continuing wear. The slightly raised edges of worn enamel enclosing the windows (Broili and Schröder, 1936: fig. 1) formed additional edges for shredding during dynamic occlusion. As the cusps were worn down, the areas for tooth-to-tooth contact increased and, consequently, occlusal pressures at the contacts decreased.

Tritylodontidae exhibit isognathy, with simultaneous occlusion on both sides, much as in certain more primitive Tritylodontoidea (Crompton, 1972: 67). Bilateral mastication is advantageous as it doubles the effective surface area for mastication and because considerable occlusal pressure can be maintained by the simultaneous action of the jaw muscles on both sides of the head (Weijs and Dantuma, 1975: 24). The unfused symphysis in tritylodontids indicates relatively little transfer of force from the working to the respective balancing side of the mandible. Mobility at the symphysis is essential for independent and simultaneous rotation of the dentaries to align properly the opposing postcanine teeth as they sequentially come into occlusion. The quadrate was capable of the prerequisite rotation about its long axis.

The articular facet for the trochlea of the quadrate is much inclined anteromedially relative to the long axis of the articular rod. In more primitive tritylodontoids such as *Diademodon* (Grine, 1977: fig. 13), the facet has a more transverse orientation. No accessory jaw articulation is developed between the squamosal and surangular in *Kayentatherium* nor is there a contact between squamosal and dentary, *contra* Fourie (1968). These structural details are consistent with the inferred propalinal pattern of jaw motion. Allin (personal communication) has suggested the existence of a syndesmotic connection between the jugal and the lateral ridge on the dentary but I find no markings on the respective bony surfaces in support of his restoration.

The principal function of the well-developed adductor jaw musculature was elevation and retraction of the mandible. By virtue of its horizontal to posteroventral fiber orientation, the posterior temporalis can be hypothesized as the principal retractor of the lower jaw. The functional importance of this muscle may account for the extension of the temporal fossa behind and below the coronoid process of the dentary. The relatively substantial increase in the height of the coronoid process, relative to the condition in *Thrinaxodon*, provided the posterior temporalis with a much increased moment arm about the jaw joint (DeMar and Barghusen, 1973). The anterior temporalis and the masseter muscles presumably acted as elevators of the mandible. The reconstructed course of the superficial masseter would indicate that a large gape could not be achieved. Protraction of the mandible during the opening phase must have been produced by the lateral pterygoids as none

of the other jaw muscles had a significant anteriorly directed vector component for this purpose.

Like that of other advanced non-mammalian synapsids, the tritylodontid masticatory apparatus features both a considerable development of the adductor jaw muscles ensheathing the coronoid process of the dentary *and* a set of greatly reduced accessory jaw bones. The joint between the articular and quadrate in tritylodontid synapsids is especially infirm and devoid of structural reinforcements against stresses produced by the jaw muscles. Crompton (1963) first emphasized this apparent enigma. He suggested the possibility of eliminating such stresses both at the jaw articulation and at the contact between the dentary and postdentary bones by a coupling of an anterodorsally aligned superficial masseter with a more or less horizontal temporalis muscle situated well above the jaw joint. These two muscles would produce a net reaction in the bite across the posterior cheek-teeth while leaving the jaw joint virtually unloaded. Tritylodontid synapsids closely approach this paradigm in the reconstructed arrangement of their adductor jaw musculature (Fig. 21). Building on recent experimental work on mammalian jaw function, Crompton and Hylander (1986) have argued that bilateral mastication was of crucial importance in minimizing the reaction forces at the jaw articulation. Hylander (1979) and Weijs (1980) have shown in a number of extant mammals that the balancing (or contralateral) jaw joint is loaded more than the working (or ipsilateral) joint during unilateral mastication. Bilateral mastication with simultaneous action of the jaw muscles on both sides, therefore, would reduce the respective loading at each jaw joint. During unilateral mastication the jaw joint on the working side would have been subjected to significant tensile forces during unilateral mastication. In terms of the bifulcral model of jaw function proposed by Bramble (1978), the posterior temporalis muscle would have acted to put the jaw joint under tension. Both the masseter and anterior temporalis muscles would produce compressive loadings at the jaw articulation and, in a force coupling, would counteract the downwardly directed rotational force produced by the posterior temporalis. The incisor region was dominated by the superficial masseter, and during significant incisor loading the jaw joints would have been subjected to compression. As argued above, such large incisal bite forces were probably not required.

Other cranial features. It is instructive to consider briefly the distribution and degree of interdigitation of cranial sutures because they reflect both the direction and relative amount of stress affecting specific regions of the skull (Herring, 1972). The circumlacrimal region of the skull shows particularly complex sutures because it played an important role in the transmission of forces from mastication as well as from the pull of the superficial masseter. The extensively developed secondary bony palate has markedly interdigitated transverse sutures between the premaxillae and maxillae and the maxillae and palatines. The areas on either side of the mid-line sutures of the component elements are raised to form a torus. This reinforcement of the mid-palatal sutures is consistent with Tatarinov's (1963) view that the secondary palate formed a structural cross-brace within the cranial framework, in addition to separating the nasal passage from the oral cavity. Generally, the sutures that extend more or less perpendicular to the mid-line of the skull are distinctly interdigitated. The lateral walls of the braincase and the zygomatic arches must have been subjected to considerable tensile stresses produced by the contraction of the powerful jaw musculature. As noted above, the temporal fascia may have been important in aiding the zygoma in resisting tensile forces produced by the masseter muscles. The temporalis musculature,

much of which arose along the ectocranial crests, must have exerted considerable tensile forces on the wall of the braincase. This may well be reflected by the extensive ossification of this region, including the formation of considerable squamous extensions of both the prootic and epipterygoid. Various primitively extracranial vessels have been partially or completely enclosed in bone (V. capitis lateralis, vessels of the "sinus canal"), presumably to protect them from the effects of muscular contraction.

The prominent maxillary sinuses and the large spaces ventrolateral to the brain may at least in part represent "void" chambers, which could have served to lighten the massive skull.

Tritylodontid synapsids exhibit numerous cranial features that are also found in extant herbivorous mammals (DuBrul, 1977):

–shortening, deepening, and (in some cases) considerable broadening of the skull;
–deep zygomatic arch;
–jaw joint placed well above the level of the upper tooth row;
–prominent diastema between incisors and cheek-teeth;
–absence of canines;
–posterior cheek-teeth placed well back;
–origin of masseter muscles placed forward;
–dentary with tall ascending ramus.

The placement of the jaw joint well above the level of the occlusal plane, the forward shift of the masseter origin, and the posterior extension of the cheek-tooth row all serve to increase the mechanical efficiency of the jaw musculature and, therefore, the bite force across the posterior portion of the tooth row. Tritylodontids differ from mammalian herbivores in having a much expanded temporal fossa and a tall coronoid process. These differences can be related to the selective elaboration in the former of the temporalis musculature that produced the posteriorly directed power stroke.

Hearing. The pronounced reduction in the size of the accessory jaw bones and the diminutive quadrate suggests that their function as elements of the jaw suspensorium was no longer their primary role. The detailed, point-by-point similarity between the postdentary bones of *Bienotherium* and the middle ear ossicles of monotremes was noted by Hopson (1966: 445). The articular with its recurved retroarticular process is directly comparable to the embryonic mammalian malleus with its recurved manubrium mallei (Fig. 23). Presley (1984: 189) expressed doubts concerning a strict homology between the retroarticular process of advanced non-mammalian synapsids and the manubrium mallei in modern mammals but his assessment was based, at least in part, on the inadequacy of preservation in previously published examples of the former feature. The similarity between the tritylodontid quadrate and the mammalian incus is not readily apparent at first glance but Hopson has argued that the peg-like posterodorsal process of the former can be compared to the crus brevis incudis. The crus longus incudis, to which the distal end of the stapes attaches, can be homologized with the posteromedially directed stapedial process of the tritylodontid quadrate. The postdentary bony rod formed an axis of rotation about which the lever arm of the retroarticular process could pivot (Hopson, 1966: fig. 8). Furthermore, the contact between the stapes and quadrate lies behind and below the axis of rotation of the quadrate, thereby creating a lever arm for that bone. This situation is directly comparable to the lever system of the mammalian auditory ossicles (Hopson, 1966: fig. 7). The quadrate pivoted about its point of attachment on the crista parotica as does the monotreme incus (Fleischer, 1973: 141).

Following Parrington (1946), Hopson (1966: fig. 6) assumed the existence of a

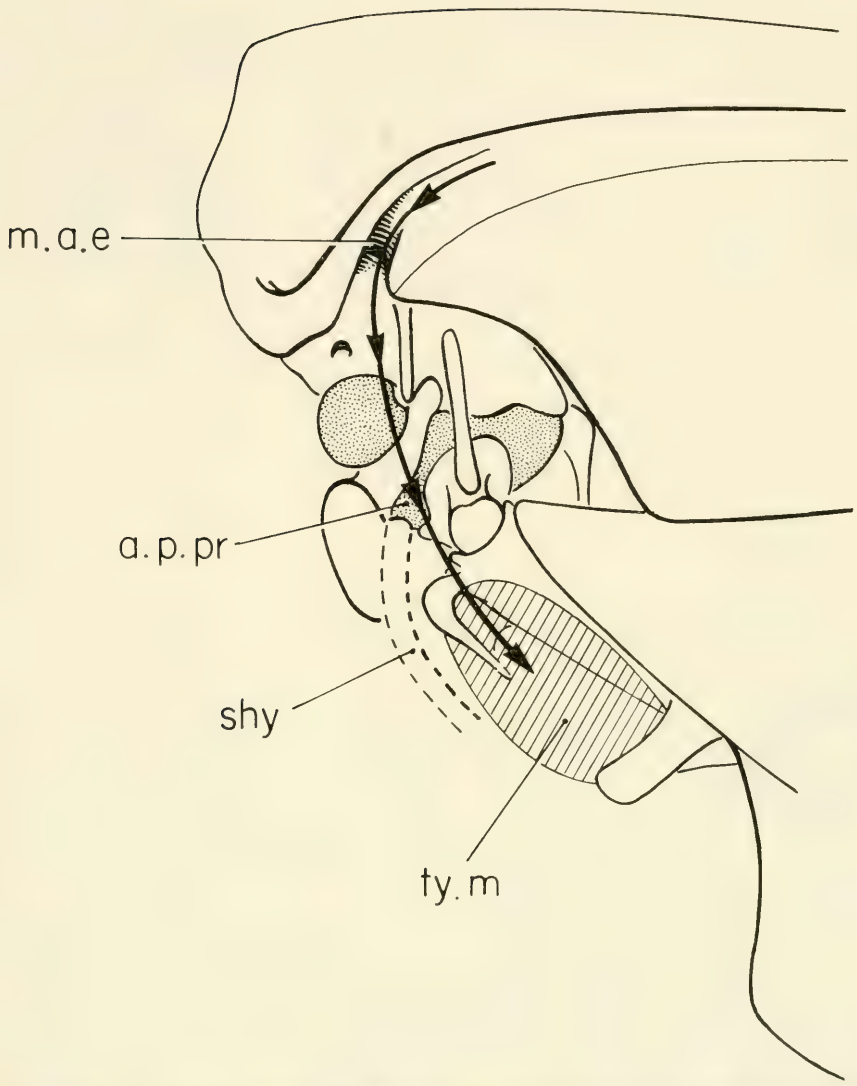


Figure 22. Diagram to illustrate the topographic relationships of the tympanic membrane (oblique hatching), external auditory meatus (arrow line), and associated bony features in *Kayentatherium wellesi.* Outline of skull based on MCZ 8812.

small post-quadratic tympanic membrane, based on the postulated course of the external auditory meatus and the alleged presence of an extrastapedial process. Allin (1975) demonstrated that there is no good evidence in support of this restoration. Indeed, as he and, more recently, Kermack *et al.* (1981: 112) have argued, such a tympanum would be extremely inefficient in receiving air-borne sound because its area would have been tiny relative to that of the fenestra ovalis. Allin instead postulated the existence of a tympanic membrane attached to the reflected lamina of the angular and to the retroarticular process. He hypothesized a con-

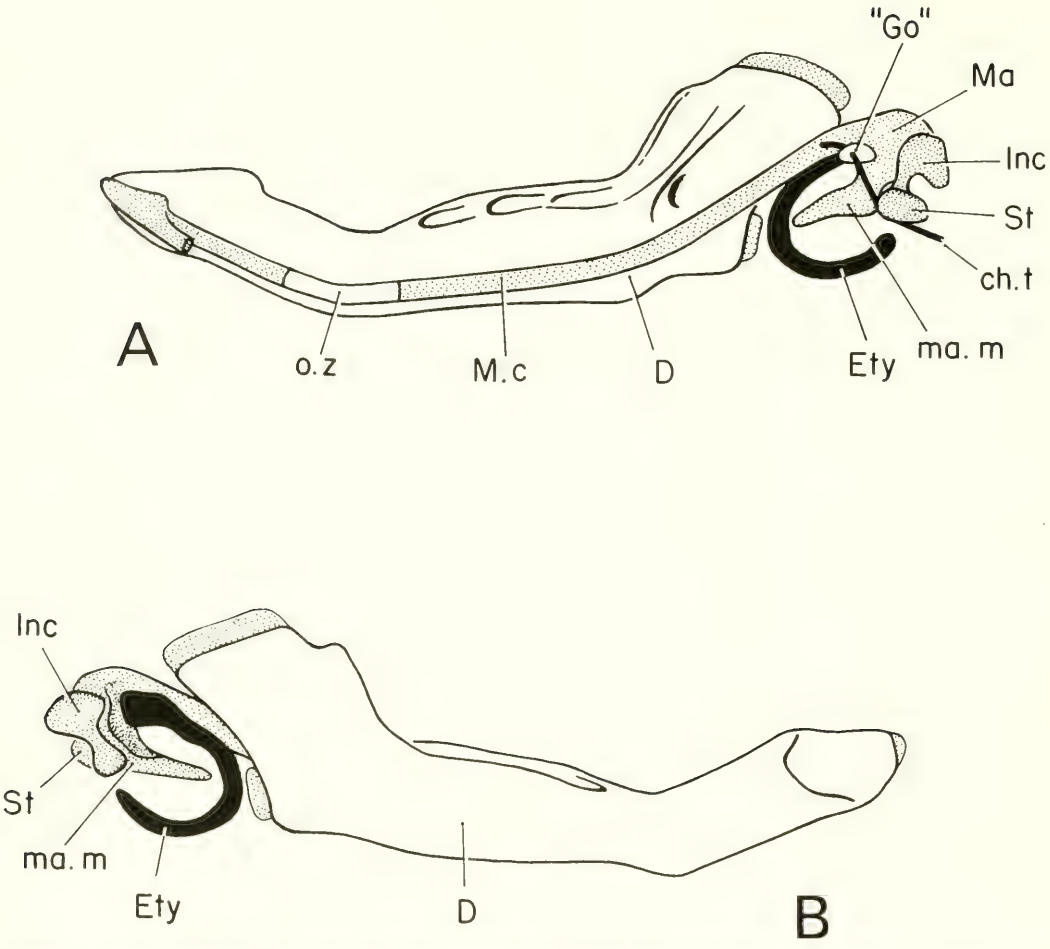


Figure 23. Outline drawings of the lower jaw, Meckel's cartilage, and associated structures in a rabbit embryo (greatest length: 45 mm), based on a model prepared by E. Gaupp. A) medial view. B) lateral view.

Abbreviations: ch.t, chorda tympani (VII); D, dentary; Ety, ectotympanic; "Go," "gonial" ossification; Inc, incus; Ma, malleus; ma.m, manubrium mallei; M.c, Meckel's cartilage; o.z, ossified zone; St, stapes. Compare with Figure 22.

ducting chain consisting of angular, articular, quadrate and stapes. Tympanic vibrations would produce a force acting on the distal extremity of the retroarticular process, initiating small rotational movements about its long axis that were transmitted to the quadrate. The quadrate would rotate slightly about its long axis and thereby activate the stapes. Angular and articular complex presumably vibrated as a unit, much as in monotremes (Aitkin and Johnstone, 1972: 247). Because of its stiffness and and mass this system of auditory ossicles would still be rather inefficient and probably worked effectively only at frequencies below one kilohertz. Indirect sound conduction from the substrate via the snout and hyoid apparatus may have been significant in addition, particularly if the hyoid arch supported the tympanic membrane posteriorly (Presley, 1984: fig. 1). The external auditory meatus, lodged in the squamosal sulcus, presumably carried on forward and below from the ventral termination of the bony sulcus (Presley, 1977; Fig. 22).

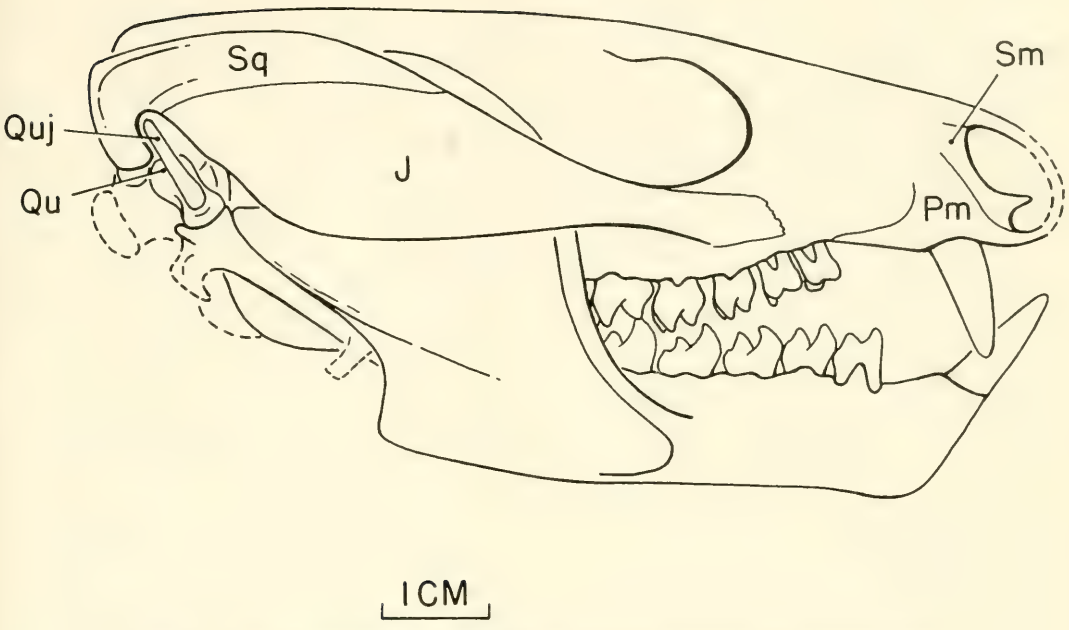


Figure 24. Skull of *Kayentatherium wellesi*, USNM 317203, reconstructed in right lateral view.

If the above restoration of the auditory complex is accurate, the tritylodontid system of sound transmission had developed a level of organization directly comparable to that of the most primitive known mammals, as inferred by Kermack *et al.* (1981).

POSSIBLE JUVENILE SPECIMENS AND RANGE IN SIZE

Among the numerous remains of small specimens of Tritylodontidae from the Kayenta Formation, a few appear to represent juvenile specimens of *Dinnebitodon* and *Kayentatherium*. Most of the other small tritylodontid remains are referable to *Oligokyphus* on the basis of dental characters (Sues, 1985b).

MCZ 8847, a right jugal and attached fragmentary maxilla with three postcanine teeth, may represent an early ontogenetic stage of *Dinnebitodon*. Its maximum length along the outer margin is 15 mm. The postcanine teeth have two buccal, three median, and two lingual cusps (Sues, 1985b: fig. 5C). The anterolingual cusp is much smaller than its successor. The completely preserved jugal closely resembles that of *Kayentatherium* (MCZ 8812, Fig. 1) in shape. The arrangement of cusps supports reference to *Dinnebitodon* rather than to *Oligokyphus* (Sues, 1985b). If correctly identified, MCZ 8847 would represent the smallest known individual of that taxon.

The upper postcanine tooth MCZ 8847 and two still uncatalogued teeth (field-numbers AR81/152 and AR81/209) have two buccal, three median, and three lingual cusps and may be referable to *Kayentatherium*.

The small dentaries MCZ 8845 and MCZ 8848 (Fig. 26A) have distinctly pointed angular processes and postcanine teeth with two principal cusps in each row. They are clearly different from the dentaries referred to *Oligokyphus* in these features (Sues, 1985b). MCZ 8848, a left dentary, is beautifully preserved. It holds two incisors, the anterior one of which is large and procumbent whereas the posterior one is smaller and less procumbent

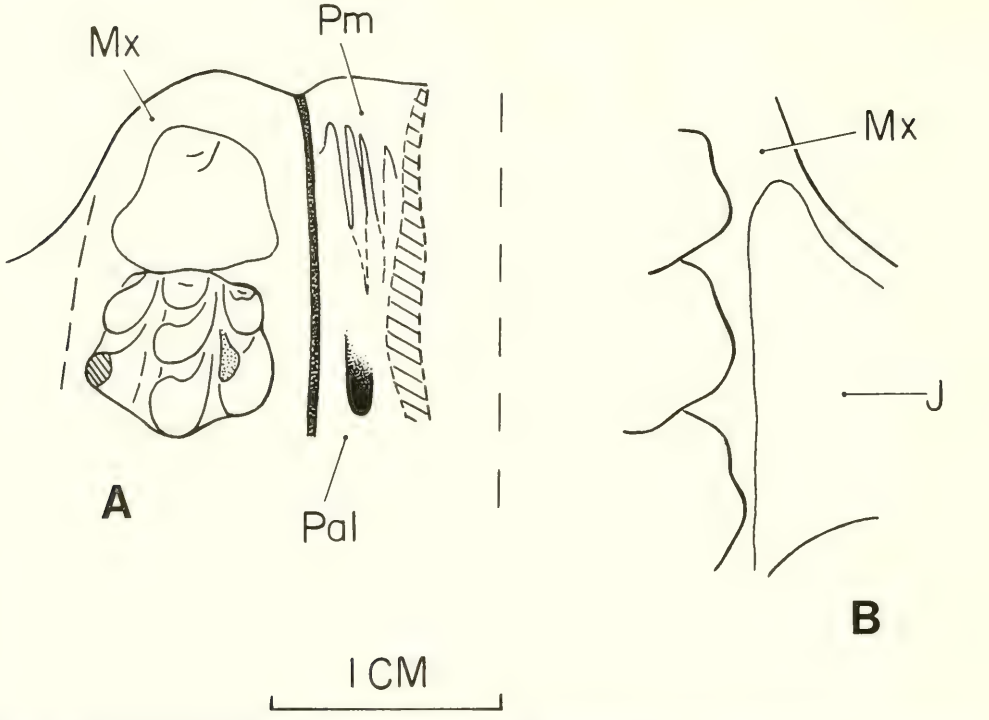


Figure 25. *Dinnebitodon amarali,* MCZ 8830. A) contact between right maxilla, palatine, and premaxilla on the palate as preserved. B) sutural contact between left jugal and maxilla in ventral view.

than its predecessor. The coronoid process slopes backward and its height equals the distance from the ventral projection of the symphysis to the angular process. The articular process is proportionately large. MCZ 8845 and MCZ 8848 possibly represent very young specimens of either *Dinnebitodon* or *Kayentatherium.*

Two tiny dentaries, MCZ 8849 (length from symphysis to angle about 6 mm) and MNA V3241 (Fig. 26B) are probably the smallest known non-mammalian synapsid jaws. They already show all the structural features characteristic of tritylodontid jaws. MCZ 8849 holds a large procumbent incisor and two postcanine teeth. The anterior cheek-tooth is raised well above the more posterior one and its anterolingual cusp is displaced forward relative to the anterobuccal cusp as on some teeth of *Oligokyphus* (Kühne, 1956: 80). MCZ 8849 and MNA V3241 represent extremely immature individuals, perhaps hatchlings. Their taxonomic affinities cannot be determined at present owing to the absence of clearly diagnostic features.

One of the specimens described by D. M. Kermack (1982: 7) but not included in her hypodigm for *Kayentatherium wellesi* was a fragment of a very large dentary. Kermack left its taxonomic status uncertain because of the considerable size difference to the holotype of *K. wellesi* (UCMP 83671). As Kermack herself noted, comparable size differences are found among modern crocodiles. The larger sample for *Kayentatherium* used in this study clearly demonstrates a range in skull length from about 80 mm (USNM 317203; Fig. 24) to about 260 mm (MCZ 8812; Fig. 1) without any structural differences of diagnostic significance. Dodson (1975: 317) observed a range in skull length in a sample of 52 skulls of *Alligator mississip-*

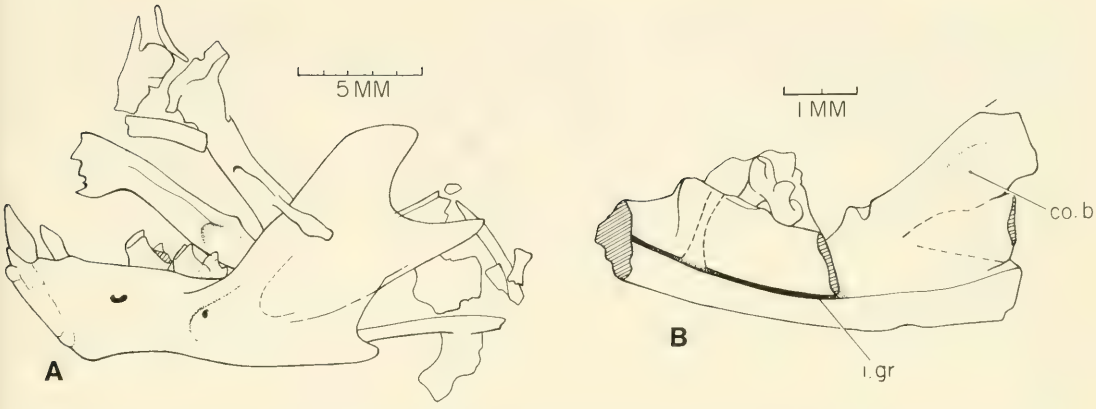


Figure 26. Juvenile specimens of indeterminate Tritylodontidae from the Kayenta Formation. A) MCZ 8848, left dentary in lateral view, with associated (?) postdentary elements. B) MNA V3241, right dentary in medial view.

piensis from 35.3 mm to 632 mm. *Bienotherium* shows size differences comparable to *Kayentatherium*. Chow (1962) described two fragmentary maxillae of *Bienotherium* and (admittedly tentatively) referred them to a new species, *B. magnum*. He notes that the length of the upper tooth row (*c.* 76 mm) is "almost twice that in *Bienotherium yunnanense*." This difference in size is almost identical to that between specimens MCZ 8811 and MCZ 8812 of *Kayentatherium*. *Bienotherium magnum* can, therefore, be synonymized with *B. yunnanense*. Hopson and Kitching (1972) have reached similar conclusions concerning the synonymy of *Likhoelia* Ginsburg, 1961 and *Tritylodontoideus* Fourie, 1962 with *Tritylodon* Owen, 1884 from the Stormberg Group of southern Africa. Tritylodontid synapsids apparently had a typically "reptilian" pattern of more or less continuous growth throughout life.

RELATIONSHIPS OF *KAYENTATHERIUM* AND *DINNEBITODON*

The Tritylodontoidea *sensu* Hopson and Kitching (1972) are characterized by the possession of postcanine teeth with buccolingually expanded crowns, which meet in complex occlusion, and by the deep dorsal emargination of the occipital portion of the squamosal (convergent with Chiniquodontidae). This represents a minimal definition of the group, which reflects the paucity of comprehensive anatomical information concerning the majority of advanced non-mammalian synapsids. Certain other diagnostic features listed by Hopson and Kitching (1972) are also found in *Cynognathus*, which Kemp (1979) placed as the sister-taxon of *Diademodon*. The Tritylodontidae Cope, 1884 (including Bienotheriidae Young, 1940) form a strictly monophyletic taxon, which can be defined by a set of derived craniodental features (Hopson and Kitching, 1972; Sues, 1986b):

- –second upper and first lower incisors greatly enlarged;
- –first lower incisor procumbent;
- –canines absent;
- –postcanine teeth with multiple roots;
- –upper postcanine teeth with three and lower postcanine teeth with two anteroposterior rows of crescent-shaped cusps;
- –prefrontal and postorbital (and postorbital bar) absent;
- –articulation between quadrate and anterior paroccipital process (crista paratica) *without* contact between quadrate and squamosal (with the possible exception of *Oligokyphus*).

Clark and Hopson (1985) and Sues (1986b) have reviewed the interrelationships of tritylodontid genera. *Kayentatherium* most closely resembles *Bienotherium* Young, 1940 from the Lower Lufeng Series of Yunnan, China. It is distinguished from the latter genus as well as from all other known Tritylodontidae by the presence of a single upper incisor, rather than two or three, in each premaxilla. *Nearctylodon broomi* Lewis, 1986 is clearly a junior synonym of *Kayentatherium wellesi* D. M. Kermack, 1982, based on the presence of a single incisor in each premaxilla and the structure of the upper postcanine teeth (personal observation). Further craniological comparisons between *Kayentatherium* and *Bienotherium* must await publication of Hopson's monographic revision of the latter genus. Certain differences in the upper postcanine teeth enumerated by D. M. Kermack (1982) are not valid (Sues, 1986b). *Dinnebitodon* apparently belongs to a more advanced clade including *Bienotheroides* Young, 1982 (upper Sha-Xi-Miao Formation, Sichuan, China) and *Bocatherium* Clark and Hopson, 1985 (La Boca Formation, Mexico). *Bienotheroides* is either late Mid-Jurassic or early Late Jurassic in age but no reliable age estimate can as yet be offered for *Bocatherium*. Derived features shared by members of this clade, which probably also includes the poorly known *Stereognathus* Charlesworth, 1855 from the Middle Jurassic (Bathonian) of the British Isles (Hopson, personal communication), are (1) exclusion of the maxilla from the side of the face by the enlarged premaxilla and lacrimal, (2) complete lateral overlap of the maxilla by the jugal (which extends down to the level of the upper tooth row), and (3) contact of the palatine and premaxilla on the palate, excluding the maxilla from participation in the formation of the secondary bony palate (Sun, 1984; Clark and Hopson, 1985; Sues, 1986a,b). Character (3) is foreshadowed to some extent in juvenile specimens of *Kayentatherium* (MCZ 8811, Fig. 6) where the premaxilla extends back on the palate between the first upper postcanine teeth. Adult specimens (MCZ 8812, MNA V3141), however, are closely similar to *Bienotherium* in that the palatal suture between the premaxilla and maxilla is placed well anterior to the upper cheek-teeth. The genera of the *Bienotheroides* clade variously show reduction in the number of cusps on the upper postcanine teeth. The upper postcanine teeth of *Dinnebitodon* can be distinguished from those of *Bienotheroides* and *Bocatherium* by the presence of but two lingual cusps and from those of *Stereognathus* by the retention of three median cusps.

APPENDIX

Abbreviations Used in Figures

An	angular
ANT	anterior
Art	articular
AT	M. temporalis, pars anterior
a.l.pro	anterior lamina of prootic
a.q.f.	anterior facet on quadrate
a.p.pr	anterior paroccipital process (crista parotica)
al.ps	parasphenoid wing
an.p	angular process of dentary
ar.c	articular complex
art.eo	articular facet for exoccipital
art.f	articular facet for quadrate trochlea
art.p	articular process of dentary
art.pro	articular facet for prootic
Bo	basioccipital
Bs	basisphenoid
BUC	buccal
Co	coronoid
Co.o	occipital condyle
c.i.o	infraorbital canal
c.i.o.l	"lacrimal branch" of infraorbital canal
c.r.t	crypt for replacement teeth
c.sm	canal in septomaxilla
co.b	boss for coronoid
co.p	coronoid process of dentary
cr.sa	sagittal crest
D	dentary

DM	M. masseter, pars profundus
DORS	dorsal
d.ch	depression for chiasma
d.g.s-p	depression for sphenopalatine ganglion
d.la	dorsal lamina of quadrate
d.m.e	depression on epipterygoid
d.m.r	depression for M. rectus capitis
d.p	dorsal process of articular
d.p.i	depression below processus intrafenestralis
d.p.pm	dorsal process of premaxilla
EP	M. pterygoideus externus (seu lateralis)
Ept	epipterygoid
e	enamel covering
F	frontal
f.cb	facet for ceratobranchial
f.c.i.o.l	foramen for "lacrimal branch" of infraorbital canal
f.d	foramen dentale
f.inc	incisive foramen
f.i.o	exit for branch of infraorbital canal
f.j	jugular foramen
f.la.l	foramen in posterolateral flange
f.m-f	maxillo-facial foramen
f.mas	masseteric fossa
f.me	mental foramen
f.o-n	orbitonasal foramen
f.ov	fenestra ovalis
f.pal.m	greater palatine foramen
f.pal.mi	lesser palatine foramen
f.p.t	posttemporal fenestra
f.pt-p	foramen pterygo-paroccipitale
f.s-p	sphenopalatine foramen
f.v	foramen for V. cerebralis media
fa	facet on quadrate
fi	orbital fissure
fl.pt	flange on pterygoid
fo	foramen
fo.ch.t	foramen for chorda tympani
fo.l	lacrimal foramen
fo.p	posterior foramen in squamosal sulcus
fo.sm	foramen in septomaxilla
I	incisor
i.gr	"internal groove" on dentary
i.m	insertion of superficial masseter muscle
i.m.t	insertion of anterior temporalis muscle
int.n	internal narial opening
ipt.fe	interpterygoid vacuity
J	jugal
La	lacrimal
LAT	lateral
l.la	posterolateral flange of prootic
l.r	lateral ridge on dentary
la.re	reflected lamina of angular
MED	medial
Mx	maxilla
m.a.e	sulcus for external auditory meatus
m.p.q	stapedial process of quadrate
m.r	medial ridge on dentary
mx.r	maxillary recess
N	nasal
n.d	notch for dens
np.cr	nasopalatine crest
Os	orbitosphenoid
o.a	posterior rim of retroarticular process
P	parietal
Pal	palatine
PC	postcanine tooth
Pm	premaxilla
POST	posterior
Pra	prearticular
Pro	prootic
Ps	parasphenoid
Pt	pterygoid
PT	M. temporalis, pars posterior
p.d	horizontal ridge on articular
p.d.tr	trough for postdentary bones
p.hy.c	process for hyoid attachment
p.int	processus intrafenestralis
p.mus	processus muscularis
p.p.pr	posterior paroccipital process
p.ret	retroarticular process
ps.cr	parasphenoid crest
pt.fl	lateral (transverse) flange of pterygoid
Qu	quadrate
Quj	quadratojugal
q.r.ept	quadrate ramus of epipterygoid
r.d	diastemal ridge on dentary
r.qj	recess for quadratojugal

ro.bs	basisphenoid rostrum
SM	M. masseter, pars superficialis
Sm	septomaxilla
Sq	squamosal
s.s.i	space for nasal septum
s.tu	sella turcica
s.v.n	sulcus for Vidian nerve
shy	stylohyal
si.mx	maxillary sinus
st.f	stapedial groove on quadrate
sy.m	mandibular symphysis
t.q	quadrate trochlea
ty.m	tympanic membrane
V	vomer
v.w.f.s-p	ventral margin of sphenopalatine foramen
va.f	vascular foramen
zy.r	ventral ridge on anterior root of zygoma

Roman numerals denote exits of cranial nerves.

LITERATURE CITED

AITKIN, L. M., AND B. M. JOHNSTONE. 1972. Middle ear function in a monotreme: the echidna (*Tachyglossus aculeatus*). J. Exp. Zool., **180:** 245–250.

ALLIN, E. F. 1975. Evolution of the mammalian middle ear. J. Morph., **147:** 403–438.

BARGHUSEN, H. R. 1968. The lower jaw of cynodonts (Reptilia: Therapsida) and the evolutionary origin of mammal-like adductor jaw musculature. Postilla, **116:** 1–49.

———. 1986. On the evolutionary origin of the therian tensor veli palatini and tensor tympani muscles, pp. 253–262. *In* N. Hotton, III, P. D. MacLean, E. C. Roth and J. J. Roth (eds.), The ecology and biology of mammal-like reptiles. Washington, D.C.: Smithsonian Institution Press.

BONAPARTE, J. F. 1962. Descripción del cráneo y mandíbula de *Exaeretodon frenguelli* Cabrera, y su comparación con Diademodontidae, Tritylodontidae y los cinodontes sudamericanos. Publ. Mus. Munic. Cienc. Nat. y Tradit. Mar del Plata, **1**(5): 135–205.

———. 1966. Sobre los cavidades cerebral, nasal y otras estructuras del cráneo de *Exaeretodon* sp. (Cynodontia-Traversodontidae). Acta Geol. Lilloana, **8:** 5–31.

———. 1980. El primer ictidosaurio (Reptilia–Therapsida) de America del Sur, *Chalimia musteloides*, del Triásico superior de La Rioja, Argentina. Actas II Congr. Argent. Paleont. y Bioestrat. y I Congr. Latinoamer. Paleont. 1978, **1:** 123–133.

BRAMBLE, D. M. 1978. Origin of the mammalian feeding complex: models and mechanisms. Paleobiology, **4:** 271–301.

BROILI, F., AND J. SCHRÖDER. 1934. Beobachtungen an Wirbeltieren der Karrooformation. I. Zur Osteologie des Kopfes von *Cynognathus*. Sitzungsber. Bayer. Akad. Wiss. München, math.-naturw. Abt., **1934:** 95–128.

———, AND ———. 1936. Beobachtungen an Wirbeltieren der Karrooformation. XIX. Ein neuer Fund von *Tritylodon* Owen. Sitzungsber. Bayer. Akad. Wiss. München, math.-naturw. Abt., **1936:** 187–228.

BROOM, R. 1911. On the structure of the skull in cynodont reptiles. Proc. Zool. Soc. London, **1911:** 893–925.

BUTLER, P. M. 1939. The post-canine teeth of *Tritylodon longaevus* Owen. Ann. Mag. Nat. Hist., London, (11)**4:** 514–520.

CALLAHAN, J. T. 1951. The geology of the Glen Canyon Group of the Echo Cliffs Region, Arizona. Plateau, **23:** 49–57.

CHOW, M. 1962. A tritylodontid specimen from Lufeng, Yunnan. Vert. Palasiat., **6:** 365–367.

CLARK, J. M., AND D. E. FASTOVSKY. 1986. Vertebrate biostratigraphy of the Glen Canyon Group in northern Arizona, pp. 285–301. *In* K. Padian (ed.), The beginning of the age of dinosaurs. New York: Cambridge University Press.

———, AND J. A. HOPSON. 1985. Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of the Tritylodontidae. Nature, **315:** 398–400.

CLUVER, M. A. 1971. The cranial morphology of the dicynodont genus *Lystrosaurus*. Ann. S. Afr. Mus., **56:** 155–274.

COLBERT, E. H. 1981. A primitive ornithischian dinosaur from the Kayenta Formation of Arizona. Bull. Mus. N. Ariz., **53:** 1–61.

CROMPTON, A. W. 1955. On some Triassic cynodonts from Tanganyika. Proc. Zool. Soc. London, **125:** 617–669.

———. 1958. Cranial morphology of a new genus and species of ictidosaurian. Proc. Zool. Soc. London, **130:** 183–216.

———. 1963. On the lower jaw of *Diarthrognathus* and the origin of the mammalian lower jaw. Proc. Zool. Soc. London, **140:** 697–753.

———. 1964. On the skull of *Oligokyphus*. Bull. Brit. Mus. (Nat. Hist.), Geol., **9:** 67–82.

———. 1972. Postcanine occlusion in cynodonts and tritylodontids. Bull. Brit. Mus. (Nat. Hist.), Geol., **21:** 29–71.

———, AND F. ELLENBERGER. 1957. On a new cynodont from the Molteno Beds and the origin of tritylodontids. Ann. S. Afr. Mus., **44:** 1–14.

———, AND W. L. HYLANDER. 1986. Changes in mandibular function following the acquisition of a dentary-squamosal articulation, pp. 263–282. *In* N. Hotton, III, P. D. MacLean, E. C. Roth and J. J. Roth (eds.), The ecology and biology of

mammal-like reptiles. Washington, D.C.: Smithsonian Institution Press.

———, AND A.-L. SUN. 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon*. Zool. J. Linn. Soc., **85:** 99–119.

DEMAR, R., AND H. R. BARGHUSEN. 1973. Mechanics and evolution of the synapsid jaw. Evolution, **26:** 622–637.

DODSON, P. 1975. Functional and ecological significance of relative growth in *Alligator*. J. Zool., London, **175:** 315–355.

DUBRUL, L. E. 1977. Early hominid feeding mechanisms. Amer. J. Phys. Anthr., **47:** 305–320.

EISENBERG, N. A., AND A. G. BRODIE. 1965. Antagonism of temporal fascia to masseteric contraction. Anat. Rec., **152:** 185–192.

ENLOW, D. H. 1982. Handbook of facial growth. 2nd edition. Philadelphia: W. B. Saunders Co., xiii + 486 pp.

ESTES, R. 1961. Cranial anatomy of the cynodont reptile *Thrinaxodon liorhinus*. Bull. Mus. Comp. Zool., **125:** 165–180.

FLEISCHER, G. 1973. Studien am Skelett des Gehörorgans der Säugetiere einschliesslich des Menschen. Säugetierk. Mitt., **21:** 131–239.

FOURIE, S. 1968. The jaw articulation of *Tritylodontoideus maximus*. S. Afr. J. Sci., **64:** 255–265.

———. 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. Ann. S. Afr. Mus., **65:** 337–400.

GAUPP, E. 1905. Das Hyobranchialskelet der Wirbeltiere. Anat. Hefte, Ergebnisse, **14:** 808–1048.

GINSBURG, L. 1962. *Likhoelia ellenbergeri*, tritylodonte du Trias supérieur du Basutoland (Afrique du Sud). Ann. Paléont., **48:** 179–194.

GREGORY, W. K. 1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., **27:** 1–524.

GRINE, F. E. 1977. Postcanine tooth function and jaw movement in the gomphodont cynodont *Diademodon* (Reptilia: Therapsida). Palaeont. Afr., **20:** 123–135.

HAHN, G. 1981. Zum Bau der Schädel-Basis bei den Paulchoffatiidae (Multituberculata; Ober-Jura). Senckenberg. leth., **61:** 227–245.

HARSHBARGER, J. W., C. A. REPENNING, AND J. H. IRWIN. 1957. Stratigraphy of the Uppermost Triassic and the Jurassic rocks of the Navajo Country. U.S. Geol. Surv., Prof. Pap., **291:** iv + 74 pp.

HERRING, S. W. 1972. Sutures—a tool in functional cranial analysis. Acta anat., **83:** 222–247.

HOPSON, J. A. 1964. The braincase of the advanced mammal-like reptile *Bienotherium*. Postilla, **87:** 1–30.

———. 1966. The origin of the mammalian middle ear. Amer. Zool., **6:** 437–450.

———, AND J. W. KITCHING. 1972. A revised classification of cynodonts (Reptilia: Therapsida). Palaeont. Afr., **14:** 71–85.

HYLANDER, W. L. 1979. An experimental analysis of temporomandibular joint reaction forces in macaques. Amer. J. Phys. Anthr., **51:** 433–456.

JENKINS, F. A., JR. 1984. A survey of mammalian origins, pp. 32–47. *In* P. D. Gingerich and C. E. Badgley (eds.), Mammals. Notes for a short course. Studies in Geology 8. Knoxville: University of Tennessee, Department of Geological Sciences.

———, A. W. CROMPTON, AND W. R. DOWNS. 1983. Mesozoic mammals from Arizona: new evidence on mammalian evolution. Science, **222:** 1233–1235.

KEMP, T. S. 1979. The primitive cynodont *Procynosuchus*: functional anatomy of the skull and relationships. Phil. Trans. Roy. Soc. London, B, **285:** 73–122.

———. 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. J. Zool. London, **191:** 193–239.

———. 1982. Mammal-like reptiles and the origin of mammals. London: Academic Press, xiv + 363 pp.

———. 1983. The relationships of mammals. Zool. J. Linn. Soc., **77:** 353–384.

KERMACK, D. M. 1982. A new tritylodontid from the Kayenta Formation of Arizona. Zool. J. Linn. Soc., **76:** 1–17.

KERMACK, K. A., F. MUSSETT, AND H. W. RIGNEY. 1973. The lower jaw of *Morganucodon*. Zool. J. Linn. Soc., **53:** 87–175.

———, ———, AND ———. 1981. The skull of *Morganucodon*. Zool. J. Linn. Soc., **71:** 1–158.

KIELAN-JAWOROWSKA, Z. 1970. Unknown structures in multituberculate skull. Nature, **226:** 974–976.

———, C. POPLIN, R. PRESLEY, AND A. DE RICQLÈS. 1984. Preliminary note on multituberculate cranial anatomy studied by serial sections, pp. 123–128. *In* W.-E. Reif and F. Westphal (eds.), Third symposium on Mesozoic terrestrial ecosystems, short papers. Tübingen, Attempto Verlag.

———, R. PRESLEY, AND C. POPLIN. In press. The cranial vascular system in taeniolabidoid multituberculate mammals. Phil. Trans. Roy. Soc. London, B.

KRAUSE, D. W. 1982. Jaw movement, dental function, and diet in the Paleocene multituberculate *Ptilodus*. Paleobiology, **8:** 265–281.

KREBS, B. 1971. Evolution of the mandible and lower dentition in dryolestids, pp. 89–102. *In* D. M. Kermack and K. A. Kermack (eds.), Early mammals. London: Academic Press.

KUHN, H.-J. 1971. Die Entwicklung und Morphologie des Schädels von *Tachyglossus aculeatus*. Abh. Senckenberg. Naturf. Ges., **528:** 1–224.

KÜHNE, W. G. 1943. The dentary of *Tritylodon* and the systematic position of the Tritylodontidae. Ann. Mag. Nat. Hist., London, (11)**10:** 589–601.

———. 1956. The Liassic therapsid *Oligokyphus*.

London: Trustees of the British Museum, x + 149 pp.

LEWIS, G. E. 1986. *Nearctylodon broomi*, the first Nearctic tritylodont. pp. 295–304. *In* N. Hotton, III, P. D. Maclean, J. J. Roth and E. C. Roth (eds.), The ecology and biology of mammal-like reptiles. Washington, D.C.: Smithsonian Institution Press.

———, J. H. IRWIN, AND R. F. WILSON. 1961. Age of the Glen Canyon Group (Triassic and Jurassic) on the Colorado Plateau. Bull. Geol. Soc. Amer., **72:** 1437–1440.

OLSEN, P. E., AND H.-D. SUES. 1986. Correlation of continental Late Triassic and Early Jurassic sediments, and patterns of the Triassic-Jurassic tetrapod transition, pp. 321–351. *In* K. Padian (ed.), The beginning of the age of dinosaurs. New York: Cambridge University Press.

OLSON, E. C. 1968. The family Caseidae. Fieldiana, Geol., **17:** 225–349.

PARRINGTON, F. R. 1946. On the cranial anatomy of cynodonts. Proc. Zool. Soc. London, **166:** 187–197.

PATTERSON, B., AND E. C. OLSON. 1961. A triconodontid mammal from the Triassic of Yunnan, pp. 129–191. *In* International colloquium on the evolution of lower and non-specialized mammals. Brussels: Koninklijke Vlaamse Akademie voor Wetenschapen, Letteren en Schone Kunsten van Belgie.

PETERSON, F., AND N. G. PIPIRINGOS. 1979. Stratigraphic relations of the Navajo Sandstone to Middle Jurassic formations, southern Utah and northern Arizona. U.S. Geol. Surv. Prof. Pap., **1035-B:** B1–B43.

PRESLEY, R. 1977. Evolution of the tympanic membrane. Acta Anat., **99:** 304.

———. 1984. The tympanic cavity of Mesozoic mammals, pp. 187–192. *In* W.-E. Reif and F. Westphal (eds.), Third symposium on Mesozoic terrestrial ecosystems, short papers. Tübingen, Attempto Verlag.

———, AND F. L. D. STEEL. 1976. On the homology of the alisphenoid. J. Anat., **121:** 441–459.

———, AND ———. 1978. The pterygoid and ectopterygoid in mammals. Anat. Embryol., **154:** 95–110.

RENSBERGER, J. M. 1973. An occlusal model for mastication and dental wear in herbivorous mammals. J. Paleont., **47:** 515–528.

ROMER, A. S., AND L. W. PRICE. 1940. Review of the Pelycosauria. Geological Society of America, Special Papers, **28:** i–x and 1–538.

SHINDO, T. 1915. Uber die Bedeutung des Sinus cavernosus der Säuger mit vergleichend anatomischer Berücksichtigung anderer Kopfvenen. Anat. Hefte, 1. Abt., **52:** 319–495.

SIGOGNEAU-RUSSELL, D., AND D. E. RUSSELL. 1974. Étude du prémier caseidé (Reptilia, Pelycosauria) d'Europe occidentale. Bull. Mus. Nat. Hist. Natur., 3e série, **230:** 145–215.

SIMPSON, G. G. 1928. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. London: Trustees of the British Museum, x + 215 pp.

———. 1933. The ear region and foramina of the cynodont skull. Amer. J. Sci., (5)**26:** 285–294.

———. 1937. Skull structure of the Multituberculata. Bull. Amer. Mus. Nat. Hist., **73:** 727–763.

STADTMÜLLER, F. 1936. Kranium und Visceralskelett der Säugetiere, pp. 839–1016. *In* L. Bolk, E. Göppert, E. Kallius and W. Lubosch (eds.), Handbuch der vergleichenden Anatomie der Wirbeltiere, Band 4. Berlin and Vienna: Urban und Schwarzenberg.

SUES, H.-D. 1985a. The relationships of the Tritylodontidae (Synapsida). Zool. J. Linn. Soc., **85:** 205–217.

———. 1985b. First record of the tritylodontid *Oligokyphus* (Synapsida) from the Lower Jurassic of western North America. J. Vert. Paleont., **5:** 328–335.

———. 1986a. *Dinnebitodon amarali*, a new tritylodontid (Synapsida) from the Lower Jurassic of western North America. J. Paleont., **60:** 758–762.

———. 1986b. Relationships and biostratigraphic significance of the Tritylodontidae (Synapsida) from the Kayenta Formation of northeastern Arizona, pp. 279–284. *In* K. Padian (ed.), The beginning of the age of dinosaurs. New York: Cambridge University Press.

SUN, A.-L. 1984. Skull morphology of the tritylodont genus *Bienotheroides* of Sichuan. Scientia Sin., B, **27:** 970–984.

TATARINOV, L. P. 1963. Novyy pozdnepermskiy terotsefal. Paleont. Zh., **1963:** 76–94.

WATSON, D. M. S. 1911. The skull of *Diademodon*, with notes on those of some other cynodonts. Ann. Mag. Nat. Hist., (8)**12:** 217–228.

———. 1942. On Permian and Triassic tetrapods. Geol. Mag., **49:** 81–116.

WEIJS, W. A. 1980. Biomechanical models and the analysis of form: a study of the mammalian masticatory apparatus. Amer. Zool., **20:** 707–719.

———, AND R. DANTUMA. 1975. Electromyography and mechanics of mastication in the albino rat. J. Morph., **146:** 1–34.

YOUNG, C. C. 1940. Preliminary note on the Mesozoic mammals of Lufeng, Yunnan, China. Bull. Geol. Soc. China, **20:** 93–111.

———. 1947. Mammal-like reptiles from Lufeng, Yunnan, China. Proc. Zool. Soc. London, **117:** 537–597.

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Labroid Intrarelationships Revisited: Morphological Complexity, Key Innovations, and the Study of Comparative Diversity

MELANIE L. J. STIASSNY and JEFFREY S. JENSEN

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Ornithological Gazetteers of the Neotropics (1975–).

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LABROID INTRARELATIONSHIPS REVISITED: MORPHOLOGICAL COMPLEXITY, KEY INNOVATIONS, AND THE STUDY OF COMPARATIVE DIVERSITY

MELANIE L. J. STIASSNY and JEFFREY S. JENSEN[1]

ABSTRACT. The morphological and taxonomic implications of pharyngognathy in acanthomorph fishes are clarified, and the monophyly of the pharyngognath Labroidei is established. Characters bearing upon hypotheses of labroid intrarelationships are reviewed and a single minimum length tree is presented and discussed. Morphological character transformations within the Labroidei display a disconcertingly large amount of homoplasy and, until a single highly corroborated phylogeny is available, statements about relationships within the suborder must remain tentative.

The predominance of attributes of the pharynx and pharyngeal jaw apparatus as a major locus for character data in the diagnosis of the Labroidei is discussed, and the implications of pharyngeal dominance in systematic analyses are explored. Finally, we review the concept of the key innovation of labroid pharyngeal specialization as a causal explanation for the morphologic and taxonomic diversification of the Labroidei.

INTRODUCTION

The Labroidei, as conceived by Kaufman and Liem (1982), consists of the families Cichlidae, Embiotocidae, Labridae and Pomacentridae; together they include approximately 1,800 species (5–10% of all living fishes). The many ecological and evolutionary questions posed by the existence of species-rich, adaptively multiradiate, and often narrowly endemic communities of labroid fishes in tropical marine and freshwater biotopes occupy an important place in modern evolutionary studies (Futuyma, 1979; Greenwood, 1984; Stanley, 1979; Vrba, 1980; White, 1978). Systematists, ecologists, ethologists, geneticists, functional and evolutionary morphologists alike have probably focused on this group more than on any other neoteleostean clade. Within the last decade alone numerous publications have appeared dealing with questions of labroid development (Aerts, 1982; Claeys and Aerts, 1984; Morris and Gaudin, 1982), functional morphology (e.g., Dullemeijer, 1980; Dullemeijer and Barel, 1977; Gobalet, 1980; Liem, 1980, 1986; Liem and Sanderson, 1986; Strauss, 1984; Yamaoka, 1978, 1980), intrarelationships (e.g., Kaufman and Liem, 1982; Liem and Greenwood, 1981; Morris, 1982; Rosen, personal communication; Stiassny, 1980), ethology (e.g., Barlow and Munsey, 1976; Brett, 1979); and ecology (Hixon, 1980; Laur and Ebeling, 1983; Schmitt and Coyer, 1982; Witte, 1984).

Interest has also centered on the evolutionary dynamics of these fishes. To be open to scientific discussion and evaluation, however, hypotheses concerning the operation of evolutionary processes such as modes and rates of speciation, the acquisition and role of evolutionary novelties, and niche-space utilization need a corroborated and precise theory of phylogenetic interrelationships (Eldredge and Cracraft, 1980; Lauder, 1981, 1982a; Nelson and Platnick, 1981; Wiley, 1981). The concept of a coherent labroid assemblage has only recently emerged (e.g., Kaufman and Liem, 1982; Liem and Greenwood, 1981), and we are still far from a consen-

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sus regarding the intrarelationships of this important clade.

Since the families comprising the Labroidei were originally united as the Acanthopterygii Pharyngognathy in the predarwinian classification of Müller (1843), attributes of the pharynx and pharyngeal jaw apparatus have played a singularly important role in labroid systematics. Our study further establishes the predominance of the pharyngeal jaw apparatus as the major locus for character data in the systematic diagnosis of the Labroidei and explores its possible implications in systematic analyses.

Recent research suggests that features of the pharynx, and in particular the labroid pharynx, have important evolutionary consequences not only for systematic studies, but for the diversification of the clade as well (e.g., Liem, 1973, 1980; Liem and Sanderson, 1986). It has long been speculated that intrinsic features of design can play a major role in evolution (Lauder, 1982b; Russell, 1982), and the key innovation of labroid pharyngeal specialization is a much cited explanatory case. We review the concept of the key innovation as a causal explanation for the morphological and taxonomic diversification of the Labroidei.

MATERIALS

Specimens were dissected under a Wild M-7 stereomicroscope, and drawings made with the aid of a camera lucida attachment. Osteological specimens were cleared and double stained following the procedure of Dingerkus and Uhler (1977). A complete list of materials including catalogue numbers is available from the senior author on request. Nomenclature of the muscles follows that of Winterbottom (1974) and Anker (1978). Topographical and skeletal nomenclature is based upon that of Nelson (1969), Rosen (1973) and Barel *et al.* (1976).

The following specimens were studied. Abbreviations in parentheses following species names refer to condition of specimens examined: c.s. (=cleared and double stained) skel. (=skeleton) and alc. (=alcohol preserved).

Labroidei

Cichlidae: *Acaronia nassa* (c.s., alc.), *"Aequidens" coeruleopunctatus* (c.s., alc.), *"Ae." potaroensis* (alc.), *Astatotilapia bloyeti* (c.s., alc.), *Astronotus ocellatus* (skel.), *Cichla ocellaris* (c.s., alc.), *Cichlasoma bimaculatum* (c.s., alc.), *C. (Heros) severum* (c.s.), *Crenicichla alta* (c.s., alc.), *Ctenochromis horii* (c.s., alc.), *Etroplus suratensis* (c.s., alc.), *Geophagus surinamensis* (c.s., alc.), *Hemichromis bimaculatus* (c.s., alc.), *Oreochromis mossambicus* (c.s., alc.), *Orthochromis malagarensis* (c.s.), *Paratilapia polleni* (c.s., alc.), *Pelmatochromis buettikoferi* (c.s.), *Sarotherodon galilaeus* (c.s., alc.), *Tylochromis jentinki* (c.s., alc.)

Labridae: *Bodianus diplotaenia* (alc.), *B. rufus* (c.s.), *Coris julis* (alc.), *Crenilabrus melops* (c.s., alc.), *Halichoeres poeyi* (c.s.), *Labrichthys unilineatus* (c.s., alc.), *Labroides dimidiatus* (c.s., alc.), *Labrus bergylta* (c.s., alc.), *Lachnolaimus maximus* (skel.), *Pseudojulis notospilus* (c.s.), *Scarus* sp. (c.s.), *Sparisoma* spp. (c.s.), *Symphodus rostratus* (c.s.), *Tautoga onitis* (skel.), *Tautogolabrus adspersus* (c.s., alc.), *Thalassoma bifasciatum* (c.s.)

Embiotocidae: *Cymatogaster aggregata* (c.s., alc.), *Damalichthys vacca* (c.s., alc.), *Ditrema temmincki* (c.s., alc.), *Embiotoca lateralis* (c.s., alc.), *Hyperprosopon argenteum* (c.s.), *Hysterocarpus traski* (c.s.), *Micrometrus minimus* (c.s.), *Neoditrema ransonnetti* (c.s.), *Phanerodon furcatus* (c.s., alc.), *Zalembius rosaceus* (c.s.)

Pomacentridae: *Abudefduf troschelli* (c.s., alc.), *A. saxatilis* (c.s., alc.), *Amphiprion allardi* (c.s., alc.), *Chromis atrilobata* (c.s., alc.), *C. cyaneus* (c.s., alc.), *Dascyllus albisella* (alc.), *Eupomacentrus planifer* (c.s.), *Microspathodon chrysurus* (alc.), *Neopomacentrus sindensis* (c.s., alc.), *Nexilaris taurus* (alc.), *Pomacentrus otophorus* (c.s., alc.), *P. moluccensis* (c.s.,

alc.), *Pristotis jerdoni* (c.s.), *Stegastes acapulcoensis* (c.s., alc.), *S. fuscus* (c.s., alc.)

Percomorph Outgroups

"Basal" Percoids

Centrarchidae: *Centrarchus macropterus* (c.s.), *Lepomis macrochirus* (c.s., alc.), *Micropterus dolomieui* (c.s., alc.), *M. salmoides* (alc.), *Pomoxis* sp. (c.s.)

Centropomidae: *Centropomus pectinatus* (c.s., alc.), *Lates niloticus* (c.s.)

Lutjanidae: *Lutjanus blackfordi* (skel.), *Lutjanus synagris* (c.s., alc.), *Rhomboplites aurorubens* (skel.)

Percidae: *Perca flavescens* (c.s., alc.), *Etheostoma olmstedi* (c.s., alc.)

Perchichthyidae: *Morone americana* (c.s.), *M. saxatilis* (c.s., alc.), *Perchichthys trucha* (c.s., alc.)

Serranidae: *Diplectrum radiale* (alc.), *Epinephelus striatus* (alc.), *Serranus cabrilla* (c.s., alc.), *S. fasciatus* (c.s., alc.), *S. hepatus* (c.s., alc.), *Synagrops bellus* (c.s., alc.)

Percoid Taxa "Close" to the Labroidei

Gerreidae: *Eucinostomus gula* (c.s., alc.), *Gerres cinereus* (alc.), *G. filamentosus* (c.s.), *G. poieti* (c.s.)

Haemulonidae: *Anisotremus virginicus* (skel.), *Anisotremus* sp. (c.s.), *Haemulon album* (alc.), *H. flavolineatum* (c.s., alc.), *Pomadasys crocro* (c.s., alc.)

Kyphosidae: *Kyphosus* spp. (c.s., alc.)

Lethrinidae: *Lethrinus* spp. (c.s., alc.)

Sparidae: *Boops boops* (c.s., alc.), *Crenidens crenidens* (c.s.), *Diplodus vulgaris* (c.s., alc.), *Pagellus erythrinus* (c.s., alc.)

Scorpididae: *Scorpis chilensis* (alc.), *Scorpis* sp. (c.s., alc.)

Additional Percoid Outgroups

Apogonidae: *Apogon maculatus* (c.s.), *Cheilodipterus macrodon* (c.s.)

Bramidae: *Brama dussumieri* (c.s.)

Carangidae: *Caranx crysos* (c.s.), *Decapterus macarellus* (c.s., alc.) *Trachinotus* sp. (skel.)

Cepolidae: *Cepola rubescens* (c.s., alc.)

Chaetodontidae: *Chaetodon* spp. (skel.)

Pomacanthidae: *Pomacanthus paru* (skel.)

Cirrhitidae: *Cirrhitichthys maculatus* (skel.)

Girellidae: *Girella albostriata* (c.s., alc.)

Leiognathidae: *Leiognathus klunzingeri* (c.s., alc.), *Leiognathus* sp. (c.s.)

Mastacembelidae: *Mastacembelus brachyrhinus* (c.s.)

Mullidae: *Mulloidichthys martinicus* (c.s.), *Upneus maculatus* (c.s., alc.)

Mugilidae: *Agonostomus monticola* (c.s., alc.), *Mugil curema* (c.s., alc.)

Pempheridae: *Pempheris* sp. (c.s.)

Pomatomidae: *Pomatomus saltatrix* (c.s., alc.)

Sciaenidae: *Pogonias cromis* (c.s., alc.), *Menticirrhus americanus* (c.s.), *Otolithes ruber* (c.s., alc.), *Pseudosciaena axillaris* (c.s.)

Anabantoidei

Anabantidae: *Anabas testudineus* (c.s., alc.), *Ctenopoma multispinis* (c.s., alc.), *Sandelia capensis* (c.s.)

Belontiidae: *Betta pugnax* (c.s., alc.)

Blennioidei

Blenniidae: *Blennius gattorgine* (skel.)

Pholidae: *Aplodichthys flavidus* (skel.)

Gobioidei

Eleotrididae: *Gobiomorus dormitor* (c.s., alc.)

Gobiidae: *Bathygobius soporator* (skel., c.s.), *Gillichthys mirabilis* (skel.) *Gobius niger* (skel.)

Acanthuroidei

Acanthuridae: *Acanthus chirurgus* (skel.), *A. triostegus* (skel.)

Siganidae: *Siganus* sp. (c.s.)

Balistoidei

Balistidae: *Balistes* sp. (skel.), *Melichthys ringens* (skel.)

Tetraodontidae: *Tetradon* sp. (skel.)
Diodontidae: *Diodon hystrix* (skel.)

Cyprinodontoidei

Cyprinodontidae: *Orestias cuvieri* (c.s.), *O. ispi* (c.s.)
Fundulidae: *Fundulus diaphanus* (c.s., alc.)
Atherinidae: *Atherinops* sp. (c.s.), *Menidia menidia* (c.s., alc.)

Exocoetoidei

Exocoetidae: *Exocoetus obtusirostris* (alc.), *E. volitans* (alc.), *Cypselurus cyanopterus* (skel.), *Parexocoetus brachypterus* (c.s., alc.)
Hemiramphidae: *Euleptorhamphus velox* (alc.), *Hemiramphus balao* (alc.), *H. brasiliensis* (skel.), *Hemiramphus* sp. (skel.), *Hemirhamphodon* sp. (alc.), *Oxyporhamphus micropterus similis* (alc.), *Hyporhamphus sajori* (alc.)
Belonidae: *Ablennes hians* (alc.), *Belone belone* (alc.), *Belone* sp. (skel.), *Platybelone argalus* (alc.), *Strongylura timucu* (alc.), *Tylosurus acus acus* (alc.), *T. crocodilus* (alc.)
Scomberesocidae: *Scomberesox saurus* (alc.), *Scomberesox* sp. (c.s., alc.), *Nanichthys simulans* (alc.)

METHODS

The size and intrafamilial diversity of labroid lineages, in combination with a lack of precise knowledge of intralineal relationships, makes selection of appropriate representatives problematical. For this reason, after an initial anatomical review within each major clade, we attempted to select a single taxon to represent the plesiomorphic familial condition for each of the characters or character complexes under investigation. Clearly it is not always the same taxon that bears the plesiomorphous state for each character under consideration (see also Stiassny, 1986). In addition to the data derived from the present review, a suite of characters relevant to the resolution of labroid monophyly and intrarelationships was compiled from a comprehensive literature survey. For characters that have previously appeared in the literature we offer a reassessment of their value as indicators of phylogenetic relationship along with a citation of pertinent literature. Although all of the characters cited in previous analyses, as well as those novel to this study, are considered in the Character Survey section, we have been selective in those that we entered into the final analysis of labroid intrarelationships. Typically, a character was excluded from analysis for one of the following reasons:

1) We disagree with previous homology assessments; 2) The character distribution is highly variable and/or uninformative; 3) In one case, the distribution among outgroups is so variable as to render polarity determination highly problematical. Although several characters are excluded from our analysis, we include a discussion of these characters and make explicit our rationale for exclusion in each case. For ease of critical review we have included our data matrix in Appendix 1.

Throughout the study character polarity was assessed by the Outgroup Method (Maddison *et al.*, 1984; Stevens, 1980; Watrous and Wheeler, 1981). In the absence of a well worked-out scheme of labroid interrelationships, selection of appropriate outgroup taxa poses a problem. In view of the importance of outgroup designation in an analysis of this kind we have attempted to mitigate the situation by reviewing a wide range of percomorph taxa and selecting two groups of outgroup taxa for particular attention. The first group included representatives of some of the families thought to be "primitive" or "basal" perciforms (Gosline, 1966; Johnson, 1980, 1984; Regan, 1913; Stiassny, 1981). The second group included representatives of those families that have been suggested by previous authors to be "close" to the Labroidei. This group included members of the Sparidae and Gerreidae (Stiassny, 1980, 1981), Kyphosidae (Tarp,

1952), Scorpididae (Morris, 1982), Haemulonidae and Lethrinidae (Rosen, personal communication). In addition, we examined a further range of percomorph taxa including a number of other pharyngognathous acanthomorphs. Where possible, outgroup families are represented by the most morphologically generalized of their genera available to us.

A minimum length tree for the included data was derived using the branch and bound algorithm of PAUP version 2.4 (Phylogenetic Analysis Using Parsimony, Swofford, 1985) with Farris (1972) optimization. The tree was rooted by designating a hypothetical taxon representing an outgroup possessing the presumed primitive state for all characters included. All characters were coded as two state characters (see Appendix 1) of equal weight. In addition to computing the shortest tree, alternative topologies, of which 14 are possible, were also explored using PAUP (Swofford, 1985) and MacClade version 1.0 (Maddison, 1986). For the purposes of our analysis we assumed familial monophyly for each of the component labroid families (Kaufman and Liem, 1982; Stiassny, 1980), and made no concerted effort to consistently sample the range of potential autapomorphies available for analysis. However, where a novel autapomorphy was identified we noted its presence and justified our assessment of its status. As the monophyly of the four major labroid lineages has been established previously (e.g., Kaufman and Liem, 1982), characters autapomorphic for the component taxa were not included in the intra-subordinal analysis.

LABROID MONOPHYLY AND THE CONCEPT OF PHARYNGOGNATHY

Despite a considerable amount of recent attention there remains much confusion about the morphological and taxonomic implications of what has been termed pharyngognathy in acanthomorph fishes (Kaufman and Liem, 1982; Liem and Greenwood, 1981; Morris, 1982; Rosen, personal communication). A clarification of the concept, in particular as it has been applied to labroids, provides a helpful introduction to our investigation of labroid monophyly and intrarelationships.

The complex series of modifications of the pharyngeal jaw apparatus (PJA) resulting in the emergence of the mobile upper and lower pharyngeal jaws of euteleostean fishes has been well documented (Lauder, 1983; Nelson, 1967b, 1969; Rosen, 1973). Once that euteleostean level of organization was attained, the basic components were then available for subsequent modification along an impressive array of difference lines. Within the Acanthomorpha, perhaps in reflection of the high degree of pharyngeal modification exhibited by that clade, characteristics of the PJA have played an increasingly central role in attempts to elucidate phylogenetic interrelationships (e.g., Rosen, 1973, 1985; Rosen and Parenti, 1981).

Pharyngognathy, as originally conceived, is the possession of united fifth ceratobranchials. Gunther (1880), following Müller (1843), used pharyngeal morphology to characterize the order Acanthopterygii Pharyngognathii which he defined in part by the shared possession of "lower pharyngeal bones coalesced into a single unit." Numerous authors have questioned Gunther's interpretation of phyletic integrity, which included in the group pomacentrids, labrids, embiotocids, and cichlids (=chromides of Gunther, 1880), and many have proposed alternative classifications for these taxa (e.g., Berg, 1940; Bertin and Arambourg, 1958; Greenwood *et al.*, 1966; Jordan, 1905; Norman, 1966; Regan, 1913).

More recently, however, in a series of papers using a range of different approaches, Liem and his coworkers address the problems of pharyngognathy, labroid monophyly and interrelationships (Kaufman and Liem, 1982; Lauder and Liem, 1983; Liem, 1973, 1986; Liem and Greenwood, 1981; Liem and Osse, 1975; Liem and Sanderson, 1986). One result of this

work is the growing consensus that Müller's original grouping has phyletic integrity, a notion formalized by Kaufman and Liem (1982) with the assembly of these taxa into the Suborder Labroidei.

The Labroidei of Kaufman and Liem (1982) is defined on the basis of three pharyngeal characters: 1) Junction or fusion of the two fifth ceratobranchial bones into a single unit; 2) Diarthrosis (bone to bone contact) between upper pharyngeal jaws and the basicranium; 3) Presence of the sphincter oesophagi muscle as a continuous sheet, with no dorsal subdivision.

A review of these and other pharyngeal features enables us to refine the concept of labroid monophyly, and the use of the term pharyngognathy in morphological studies. Throughout this section summary statements of characters assessed to be synapomorphic for the Labroidei are italicized.

Among acanthomorphs there exists an array of diverse lineages each with representatives in which the pharyngeal jaws are hypertrophied (relative to non-pharyngognathous members of their respective clades), and the fifth ceratobranchials comprising the LPJ are united into a single functional unit. In addition to the labroids, Liem and Greenwood (1981) and Kaufman and Liem (1982) cited members of the Anabantidae (Figs. 1E, F), Kyphosidae, Pomadasyidae, Centrarchidae, Carangidae, Sciaenidae (Fig. 1A) and Cyprinodontoidei (see also Parenti, 1984) as bearing fused or otherwise joined lower pharyngeal jaws. Actually this list should be extended to include (some but not all) members of the Gerreidae (Fig. 1C), Leiognathidae (Fig. 1D), Sparidae and Haemulonidae (Rosen, ms), Pholidichthyidae (Springer and Freihofer, 1976), Lutjanidae (Johnson, 1980) and members of the Beloniformes[2] (Figs. 2B, C).

Comparison of the pharyngeal jaws in a range of percomorph taxa illustrates that the nature of the LPJ union differs markedly within the assemblage. In the majority of percoids with a hypertrophied pharynx the LPJ is formed by the close apposition of the two fifth ceratobranchials. The union is mediated by a simple straight suture reinforced ventrally by a concentration of connective tissue. This is also the case in the anabantoids examined (Figs. 1E, F). In pharyngognath gerreids (Fig. 1C) and sciaenids (Fig. 1A), as well as in virtually all cichlids (the single exception being the autapomorphic condition in *Cichla*, discussed by Stiassny, 1982 and in press), the suture is convoluted caudally and the contralateral elements interdigitate (e.g., Fig. 3B). Among cyprinodonts both the straight suture and the interdigitating type are expressed (see figures in Rosen, 1964; Rosen and Parenti, 1981). Finally, in the non-cichlid labroids (Figs. 3A, C, D), as well as in exocoetoid beloniforms (Figs. 2B, C), there is a complete fusion of the two LPJ elements and no trace of a central sutural union is evident. The phylogenetic implications of these different modes of union within the Acanthomorpha is unclear, although in the Labroidei the condition of complete fusion is interpreted as a synapomorphy of labrids, pomacentrids and embiotocids (page 288).

In view of the mosaic distribution of this character, the presence of coalesced lower pharyngeal jaws as a defining character of labroids is, by itself, rather weak (but see page 286 for further discussion). Indeed the "tendency" towards the expression of pharyngognathy (co-occuring with hypertrophy of the PJA) would appear to be extremely widespread

[2] Due to a lack of material available for examination, we have not included members of the family Adrianichthyidae in our analysis. Details of pharyngeal morphology of these fishes are few, but some data are presented in Rosen (1964) and Rosen and Parenti (1981). The adrianichthyoids are notable among beloniforms in lacking a united and medially fused LPJ. Throughout this paper we adopted Rosen and Parenti's (1981) classification of the Beloniformes (Fig. 7; see also Collette *et al.*, 1984).

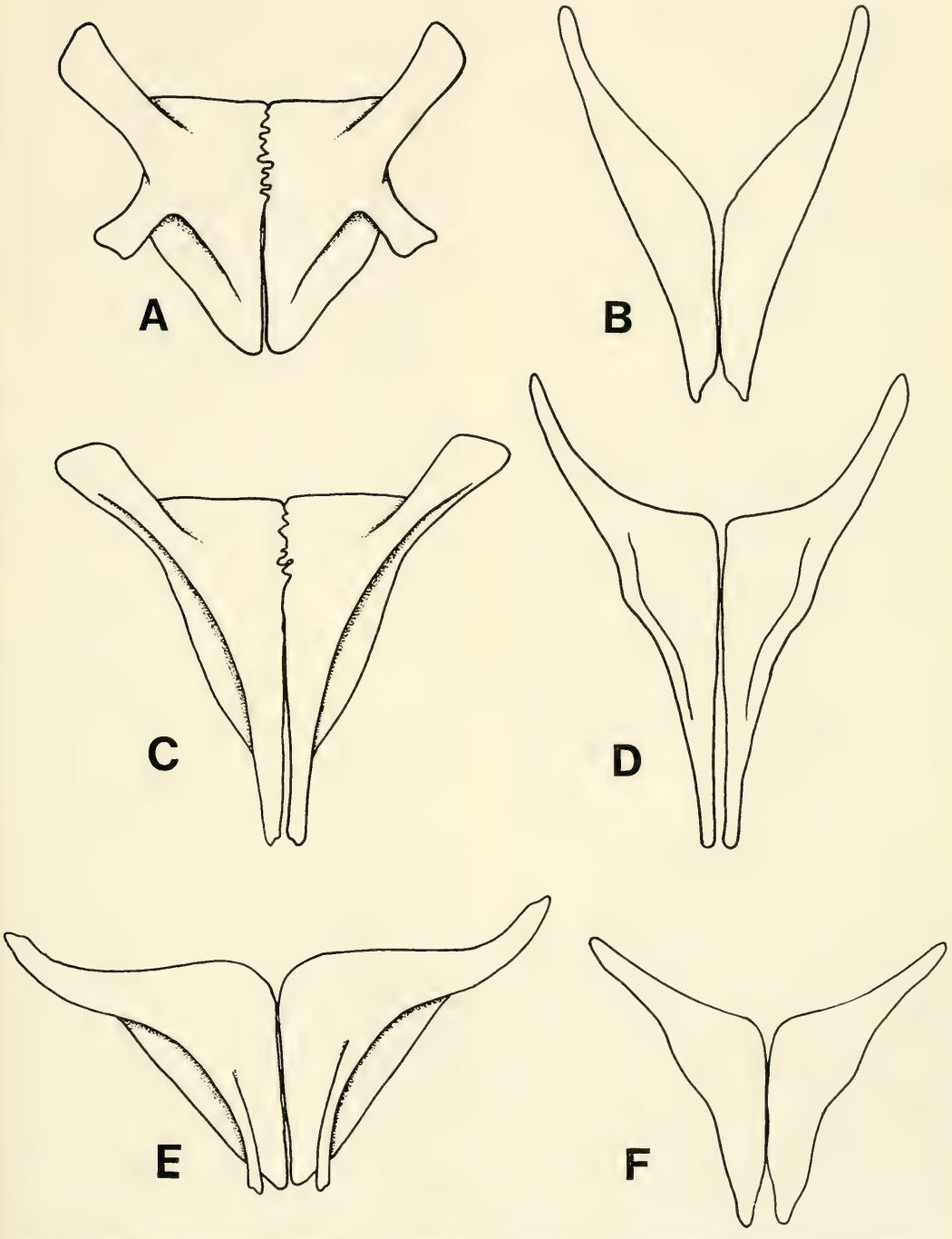

Figure 1. Lower pharyngeal jaw in ventral view. A. *Pogonias*; B. *Menticirrhus*; C. *Gerres*; D. *Leiognathus*; E. *Anabas*; F. *Sandelia.*

Abbreviations for this and the following figures are listed at the end of the text under Appendix 2.

among percomorphs, as well as in Rosen and Parenti's (1981) division II of the Atherinomorpha.

One feature of the LPJ appears to be unique (among perciforms) to the labroids and as such strengthens the claim of labroid monophyly. In all labroid taxa the LPJ bears a well-developed median keel on the ventral face of the bone (Fig. 3A–D). This blade-like keel serves as an attachment site for a part (or all, in some labrids and cichlids) of the transversus ventralis muscle (Fig. 4). Primitively among acanthomorphs the transversus ventralis is bipartite (TV V and IV), the second of these muscles (IV) passes from the fourth ceratobranchial of one side to insert on the contralateral element, thus entirely bypassing the fifth ceratobranchials (e.g., Fig. 4A). Although in a few other so-called higher percoid lineages the transversus ventralis is reduced to a single muscle (IV), in these taxa it passes between fourth ceratobranchials and has no insertion onto the LPJ keel. *The presence of a blade-like keel on the LPJ and the presumably correlated shift in insertion of part (or all) of the transversus ventralis onto that keel constitutes a synapomorphy of the Labroidei.*

In exocoetoid beloniforms a remarkably similar arrangement of pharyngeal keel and transversus ventralis insertion is present.

Primitively among perciforms the transversus dorsalis anterior muscle is bipartite and, following the nomenclature of Anker (1978), the two components are designated the m. cranio-pharyngobranchialis 2 and the m. transversus epibranchialis 2 (e.g., Figs. 5C, D). Within the Labroidei the percomorph muscle configuration has undergone a partial reduction and the *pomacentrids, embiotocids and labrids are characterized by the lack of the anterior muscle component, i.e., the m. cranio-pharyngobranchialis 2* (see Stiassny, 1980 figs. 22, 23, 24; Kaufman and Liem, 1982 fig. 2). A well-developed m. cranio-pharyngobranchialis 2 is present in all cichlid taxa (e.g., Fig. 6E). An elaboration of the percomorph configuration of the transversus dorsalis is also evident among labroids and in cichlids (Fig. 6E), pomacentrids and labrids (Kaufman and Liem, 1982; Stiassny, 1980) a third division of the muscle is developed (the m. transversus pharyngobranchialis 2; Fig. 6E). Uniquely among acanthomorphs, the embiotocid transversus dorsalis anterior muscle complex is represented by a single component (the m. transversus epibranchialis 2). The embiotocid condition could have been derived by a reduction from the primitive bipartite percomorph condition or it could represent a reduction from the tripartite state of the remaining Labroidei. Although not strictly the most parsimonious interpretation, Stiassny (1980) adopted the second alternative. She regarded the presence of a m. transversus pharyngobranchialis 2 muscle division to be synapomorphic for labroids and interpreted the absence of the division in embiotocids as a secondary loss reflecting an extension of the reductive trend already noted in the loss of the cranio-pharyngobranchialis 2 of embiotocids, labrids and pomacentrids. Following the same reasoning, and with due reservation, we concur with Stiassny (1980) in her interpretation and assess *the presence of a m. transversus pharyngobranchialis 2 division of the transversus dorsalis anterior muscle to be a synapomorphy of the Labroidei (secondarily reduced in the Embiotocidae).* However, the alternative interpretation of a cichlid/labrid/pomacentrid alignment based upon transversus elaboration is clearly posed.

According to Liem and Greenwood (1981) the Cichlidae are characterized by an additional subdivision of the m. transversus epibranchialis 2 (see Anker, 1978), resulting in a quadripartite transversus anterior muscle. The Labridae also bears a quadripartite transversus dorsalis anterior complex, but in these fishes the additional muscle part is a m. transversus epibranchialis (Stiassny, 1980). Reduction

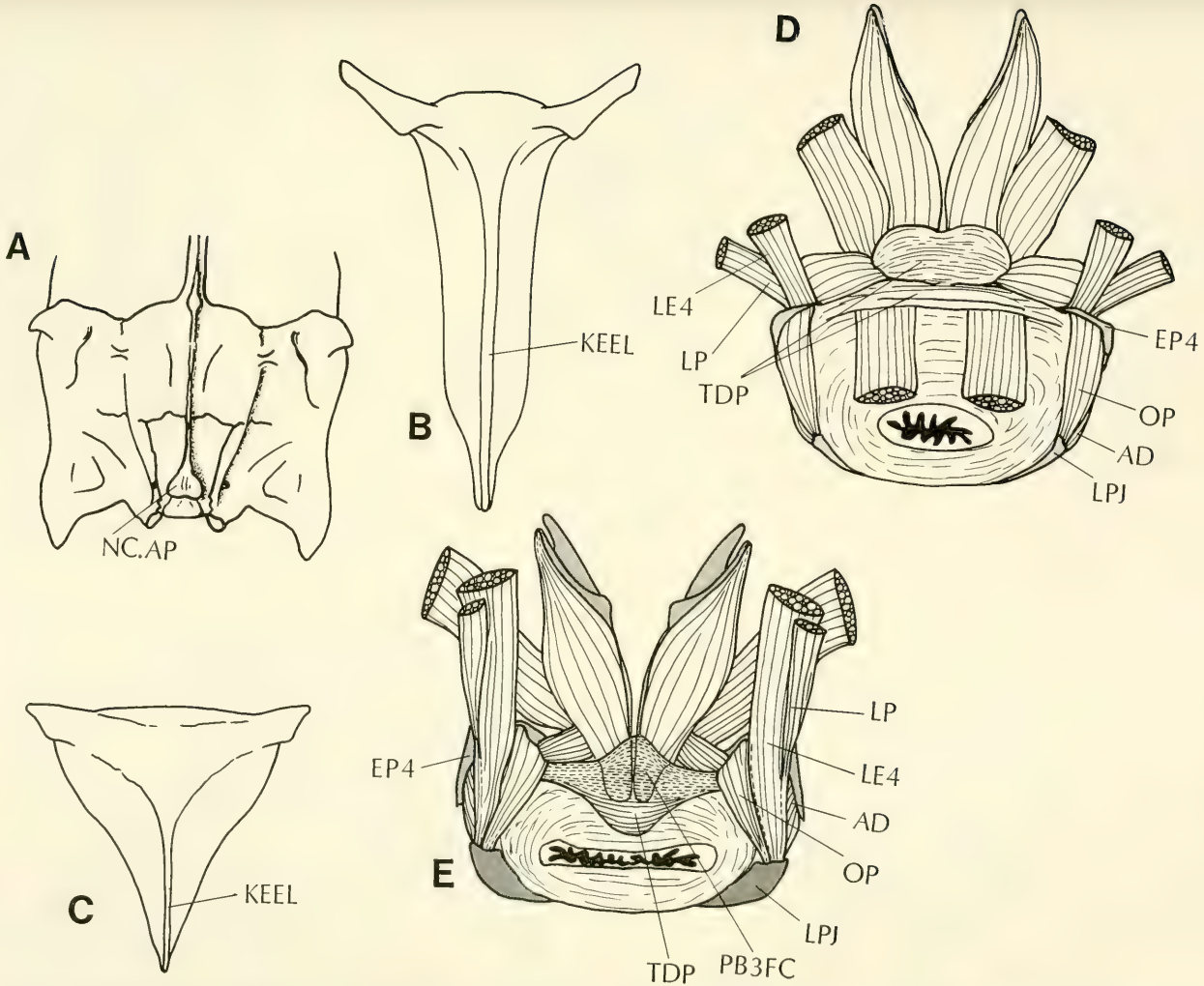

Figure 2. Aspects of the beloniform pharyngeal jaw apparatus. A. *Exocoetus* pharyngeal apophysis (ventral view); B. *Belone* LPJ (ventral view); C. *Exocoetus* LPJ (ventral view); D. *Strongylura* isolated PJA (dorsal view); E. *Exocoetus* isolated PJA (dorsal view).

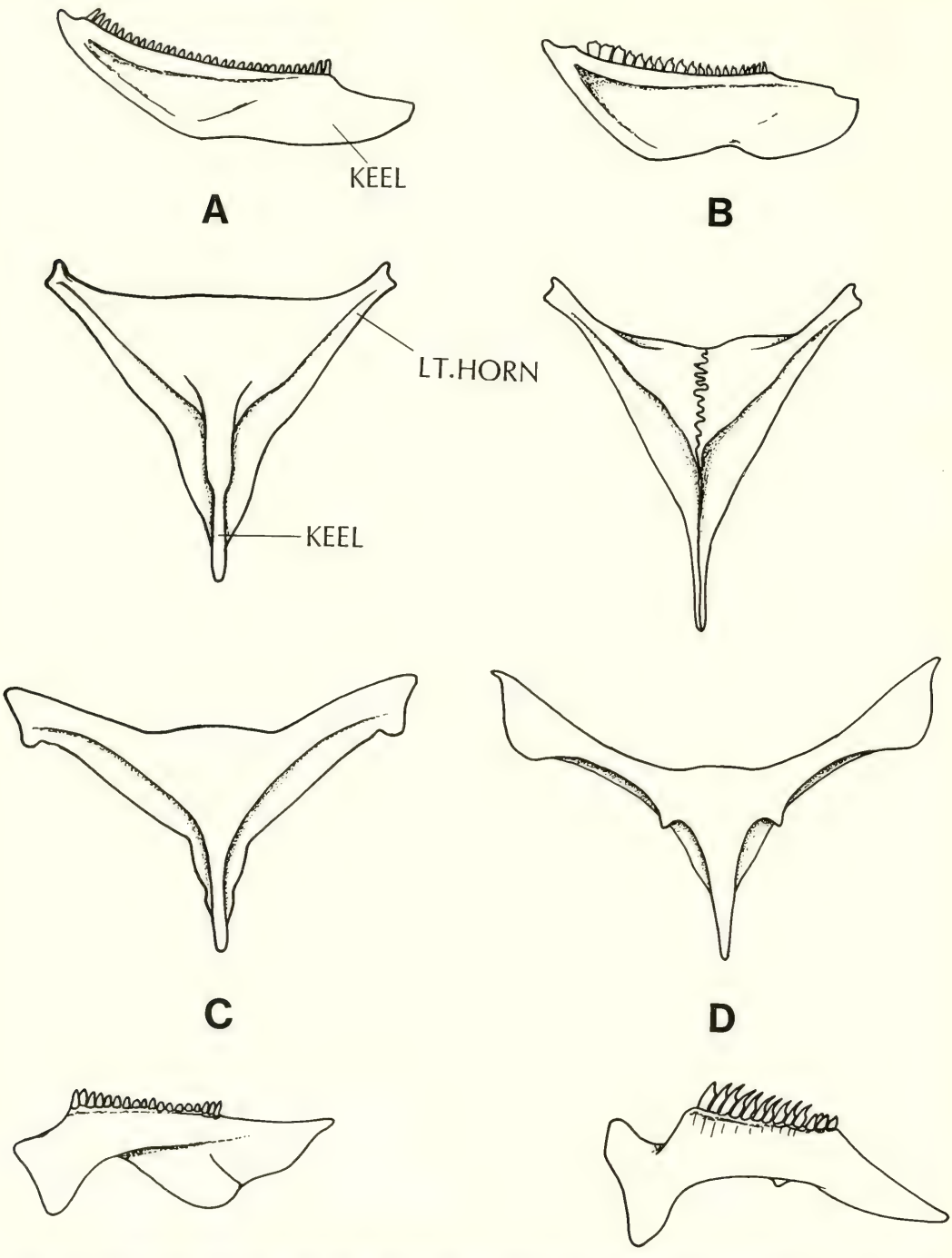

Figure 3. Lower pharyngeal jaw in lateral and ventral view. A. *Embiotoca*; B. *Astatotilapia*; C. *Labrus*; D. *Pomacentrus*.

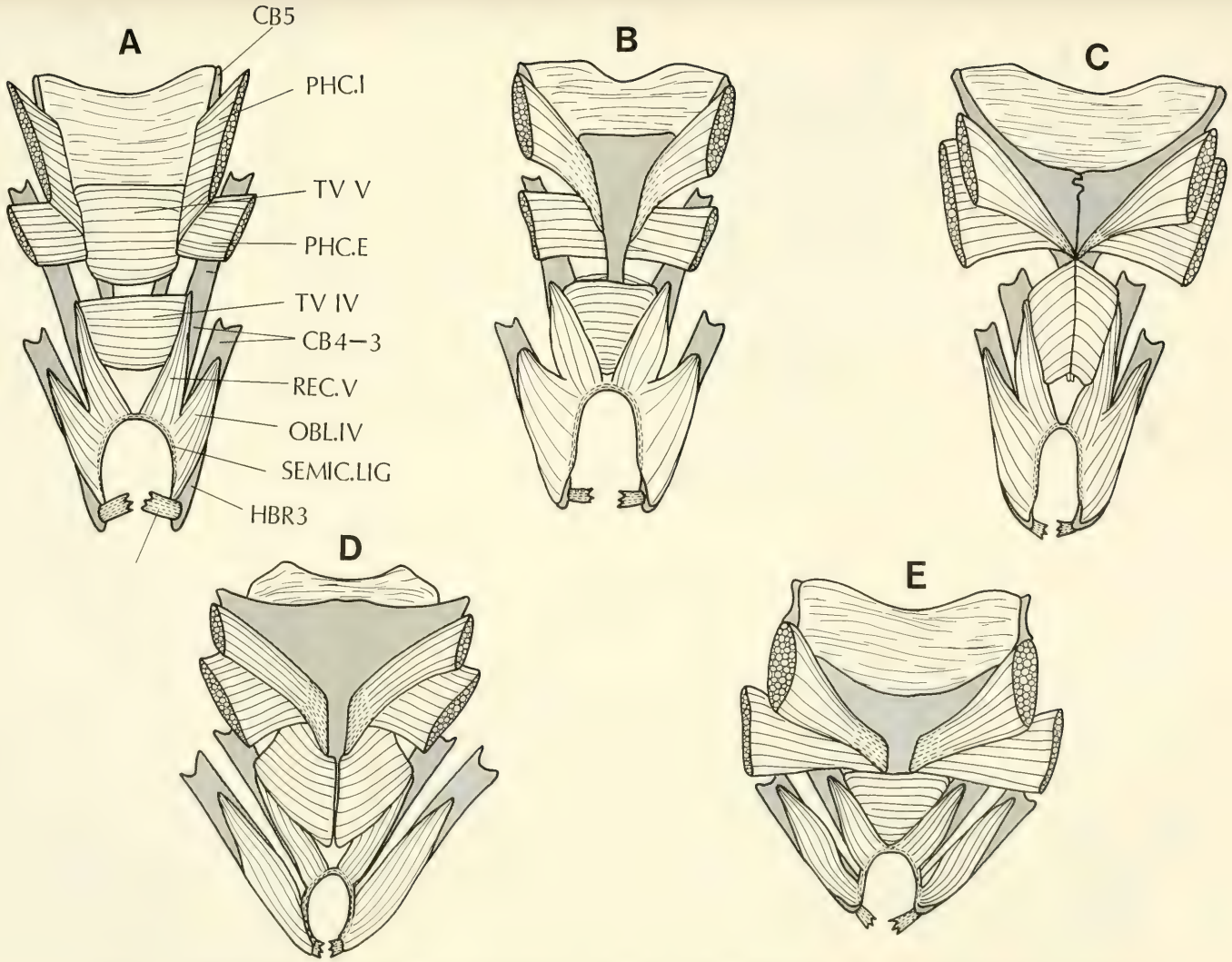

Figure 4. Ventral branchial arch musculature of: A. *Morone*; B. *Embiotoca*; C. *Astatotilapia*; D. *Labrus*; E. *Pomacentrus*, in ventral view.

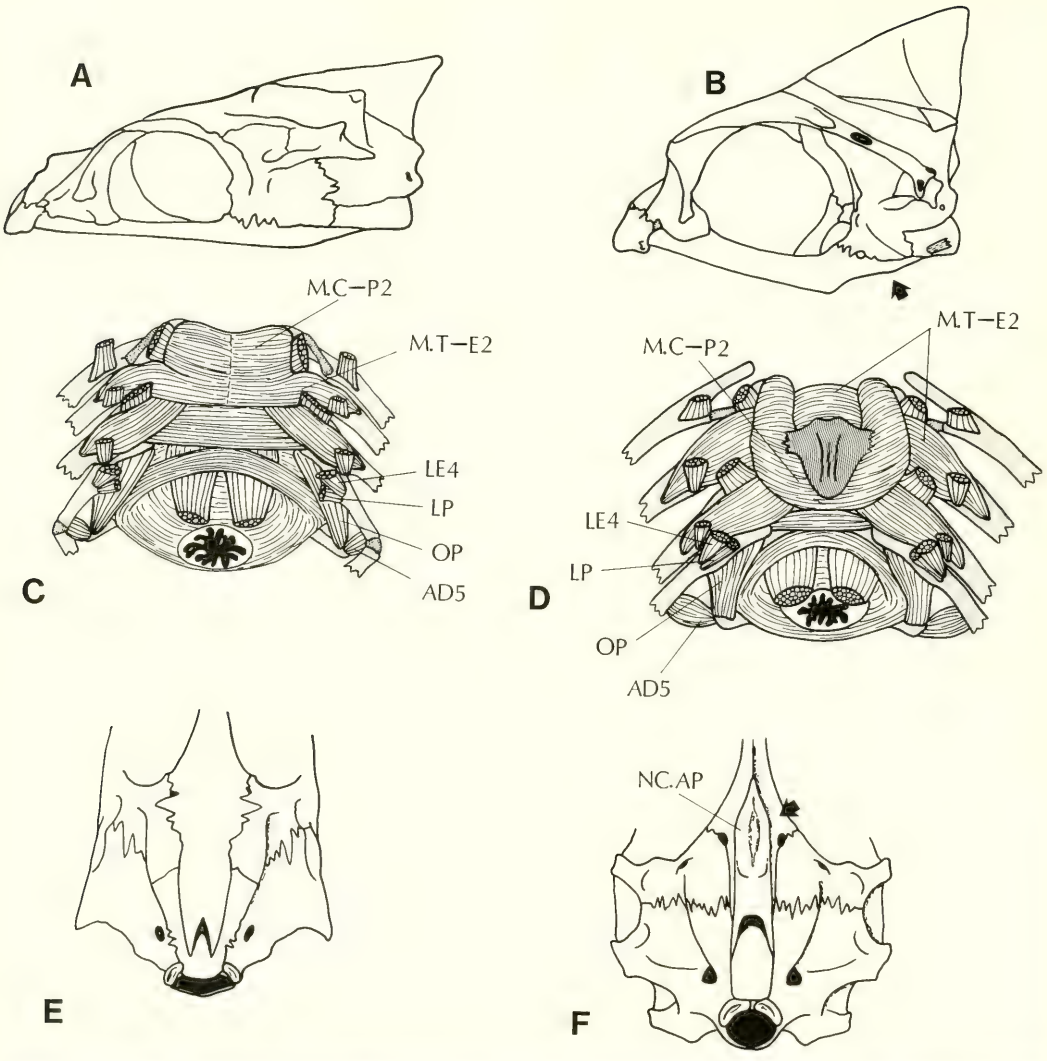

Figure 5. Aspects of the percoid pharyngeal jaw apparatus. A. *Morone* neurocranium (lateral view); B. *Diplodus* neurocranium (lateral view); C. *Morone* isolated PJA (dorsal view); D. *Diplodus* isolated PJA (dorsal view); E. *Morone* postorbital region of the neurocranium (ventral view); F. *Diplodus* pharyngeal apophysis (ventral view).

of the transversus dorsalis anterior to a single component—the m. transversus epibranchialis 2—is a synapomorphic feature of embiotocids.

Kaufman and Liem's (1982) second character, the presence in labroids of a true diarthrosis between upper pharyngeal jaws and the basicranium has been discussed by Stiassny (1980, 1982), however some additional clarification is helpful here.

In labroids the transversus dorsalis anterior and the transversus dorsalis posterior muscles do not completely overlie the raised articular facets borne on the third pharyngobranchials of the upper pharyngeal jaws (UPJ), and these bony facets are exposed (e.g., Fig. 6E; see also

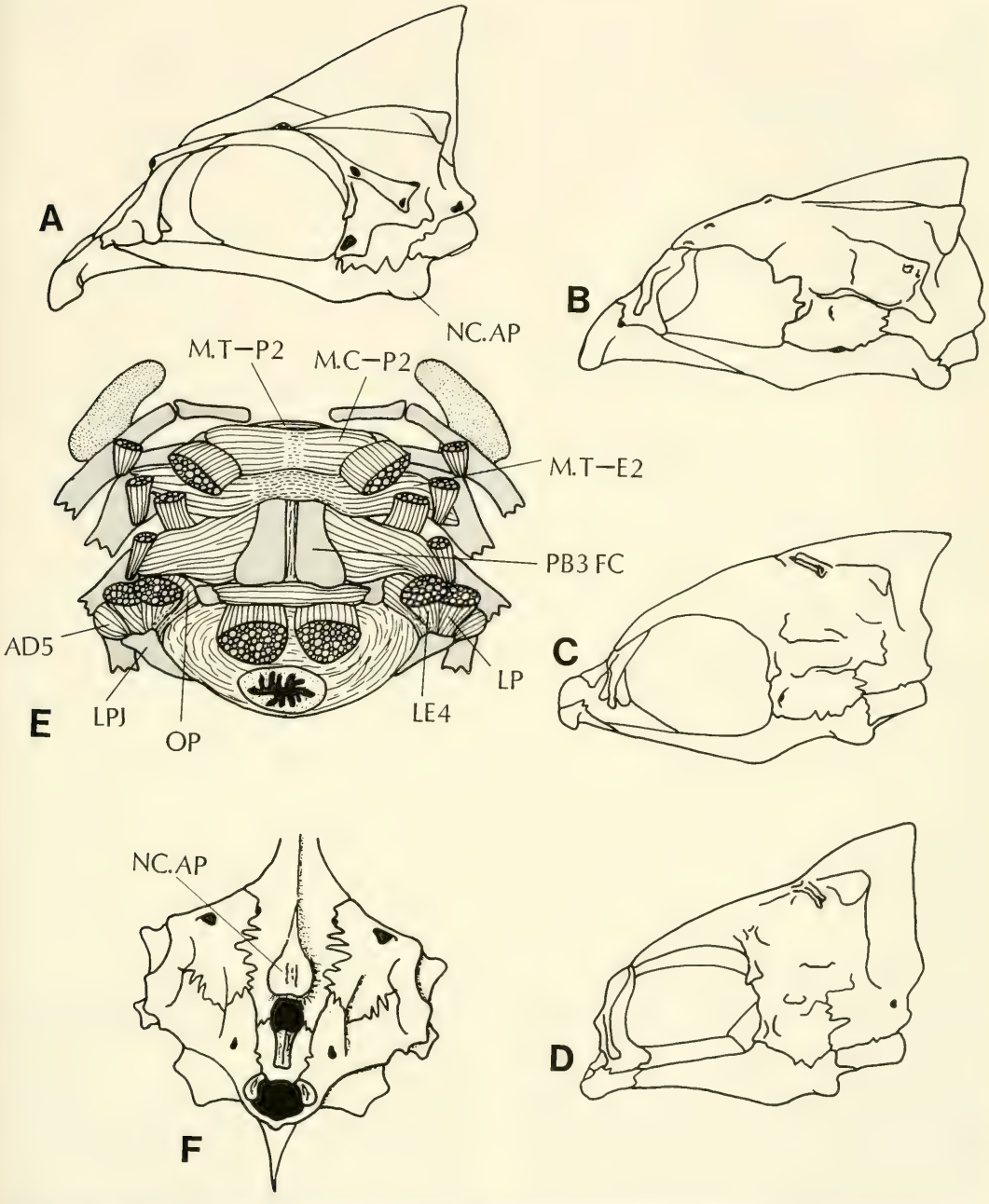

Figure 6. Aspects of the labroid pharyngeal jaw apparatus. A. *Tylochromis* neurocranium (lateral view); B. *Labrus* neurocranium (lateral view); C. *Embiotoca* neurocranium (lateral view); D. *Pomacentrus* neurocranium (lateral view); E. *Tylochromis* isolated PJA (dorsal view); F. *Tylochromis* pharyngeal apophysis (ventral view).

figures in Kaufman and Liem, 1982; Liem and Greenwood, 1981). On the skull base the LPJ facets are opposed by a raised neurocranial apophysis (Figs. 6A–D; see also Greenwood, 1978). This is not the case in "lower percoids" (e.g., *Serranus* Stiassny, 1982; *Morone*, Fig. 5C) where the entire dorsal face of the UPJ is covered by muscle and the skull base bears no articulatory or apophyseal structure (Fig. 5E). In pharyngognath members of the Gerreidae, Leiognathidae, Sciaenidae, Sparidae (e.g., Figs. 5B, D, F), and Girellidae a quite different situation pertains. In these taxa the transversus dorsalis anterior muscle complex is hypertrophied, and the cranio-pharyngobranchialis 2 forms a muscular "cushion" over the UPJ; the median connective tissue raphe, which is merely a longitudinal septum in *Morone* (Fig. 5C), is hypertrophied forming a substantial fibrous pad that overlies the muscle and is sculptured to fit closely into a grooved apophysis borne on the skull base (Figs. 5D, F). Although there is considerable variation in the form of the corresponding neurocranial apophyses, ranging from the strongly indented cup-like parasphenoid structure of *Pogonias* to the ventral thickening and reinforcement of the paraphenoid in *Diplodus* (Fig. 5F), in none of these taxa does the apophysis have the same morphology as that of labroids.

Based on these observations we consider the form of the labroid neurocranial apophysis highly characteristic of that clade. In labroids the articular surface is borne on a ventrally projecting apophysis formed in most cases by the parasphenoid and supported dorsally by the ventral margin of the prootic of each side. In some cichlids and embiotocids the basioccipitals also contribute to the articular surface of the apophysis (see Greenwood, 1978; Morris, 1982). In lateral view the apophysis of labroid fishes can clearly be seen as a rounded ventral projection (NC.AP in Figs. 6A–D). Greenwood (1978: 301) noted that the apophysis of certain labrids is structurally very similar to that of certain cichlids, but concluded that ". . . the gross morphology is quite unlike that in the cichlids." While we agree that the labrid apophysis is highly characteristic of that clade (see e.g., figs. in Rognes, 1973) we disagree that it is "quite unlike" that of other labroids. Thus, although a neurocranial apophysis of some form is commonly developed in other pharyngognath acanthomorphs, in no case is the apophysis developed in the same way or to the same extent as that described and illustrated here for the labroids. We propose that, in addition to sharing the synapomorphy of the presence of a true diarthrosis (bone to bone contact) between the neurocranial base and the third pharyngobranchials, *the labroids are further characterized by the synapomorphic presence of a ventrally projecting rounded form of the neurocranial apophysis.*

An interesting parallel is also found among beloniform fishes. In exocoetids (Exocoetidae and Hemiramphidae) a well-developed neurocranial apophysis (but formed entirely by the basioccipital bone) articulates with exposed dorsal facets on the third pharyngobranchials (Fig. 2A). The exposure of the third pharyngobranchials is brought about by a modification of the anterior portion of the transversus dorsalis posterior muscle into a thin connective tissue sheet (Fig. 2E). Contrasted with this is the condition of the complex in scomberesocids (Belonidae and Scomberesocidae) where, although a well-developed basioccipital apophysis is present on the neurocranium, articulation with the pharyngobranchial facets is interrupted by a thickened region of connective tissue of the transversus dorsalis muscle, as well as by the muscle itself (Fig. 2D).

The sphincter oesophagi muscle is subdivided in all of the nonlabroid percomorph taxa examined during the course of this investigation, and the lack of the subdivision is confirmed as being a synapomorphy of the Labroidei (Stiassny, 1980). The dorsal division of the sphincter oesophagi is greatly reduced (scombere-

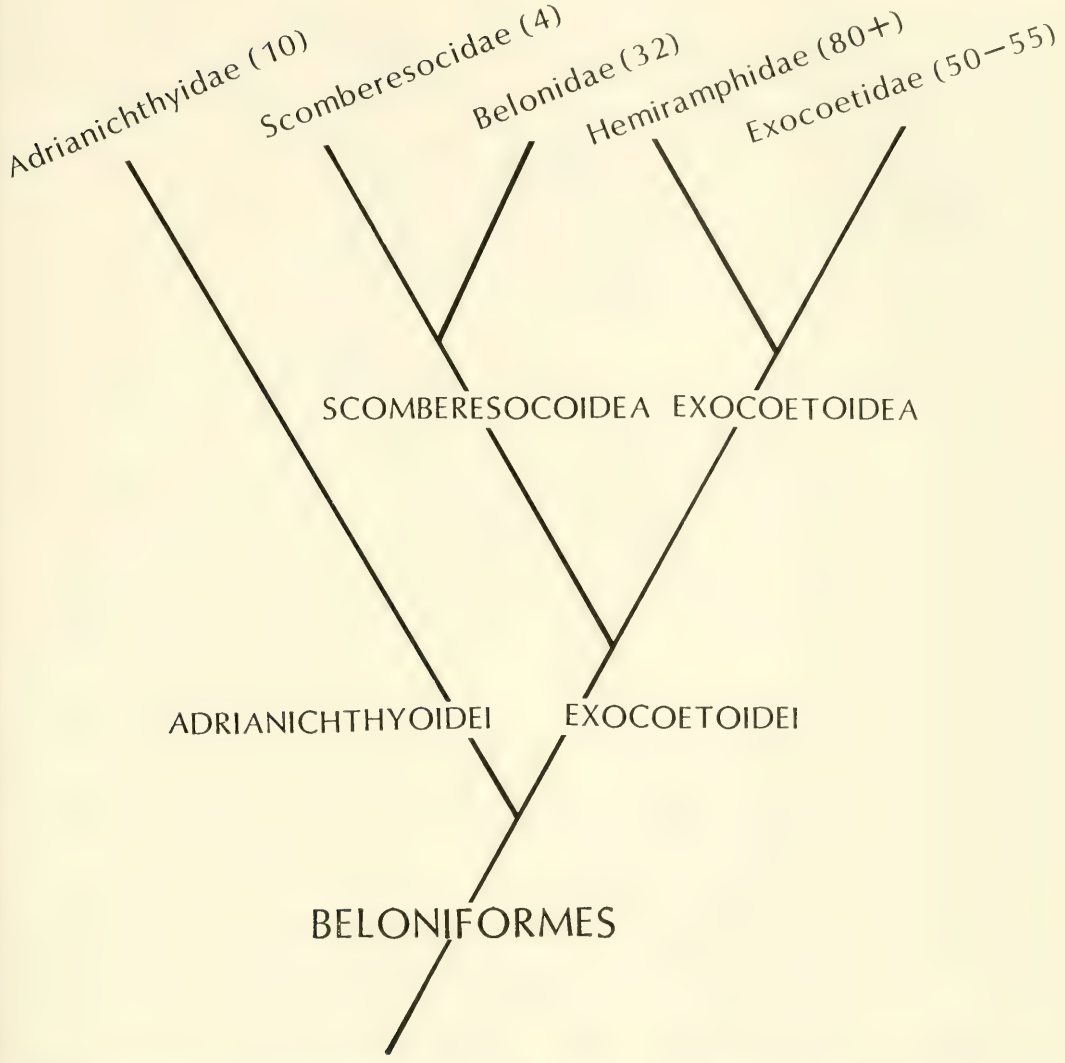

Figure 7. Cladogram of beloniform relationships, modified after Collette *et al.*, 1984. The numbers in parentheses after family names indicate number of included species.

socid), or entirely absent (exocoetid) in beloniforms. Before summarizing the principal components of this specialized labroid pharynx it is necessary to consider one further feature of the PJA.

Liem (1973) first drew attention to a fundamental difference in the muscular linkage between LPJ and neurocranium in cichlids as compared to other taxa (see also Liem, 1986). As part of the morphological basis for the adaptive radiation within the Cichlidae, Liem (1973) identified a functionally strategic shift in the insertion of the fourth levator externus muscle (le4) from the fourth epibranchial bone to the LPJ. A similar shift in levator insertion has since been found in labrids (including scarids and odacids) and embiotocids (Liem and Greenwood, 1981; Liem and Osse, 1975; Stiassny, 1980), and

the presence of this muscle sling has been thought to be central to the functional innovation of these taxa as well as being synapomorphic for the three families (Kaufman and Liem, 1982; Liem and Greenwood, 1981). The pomacentrids were thought either to entirely lack the le4/LPJ linkage (Liem and Greenwood, 1981) or possess a muscular sling in "its most primitive and incomplete configuration" (Liem, 1986: 311; see also Kaufman and Liem, 1982).

Our observations of the muscle sling in the Pomacentridae reveal a considerable amount of variation within that clade. In some taxa (e.g., *Neopomacentrus*, *Chromis* and *Amphiprion*; Fig. 8C) the configuration is much like that of other non-labroid percomorphs (e.g., Fig. 8A). While in others (e.g., *Stegastes*, *Dascyllus*, *Pomacentrus* and *Abudefduf*; Fig. 8B) the fibres of le4 are continuous, although interrupted by a fine myosept (see also Liem, 1986; Fig. 4 for the presence of a similar myosept in *Embiotoca*), with those of a division of the obliquus posterior. In those taxa in which the muscle sling is particularly well-developed (e.g., *Abudefduf* and *Stegastes*) the compound le4/obliquus posterior can be easily dissected free of the fourth epibranchial revealing a continuous connection between the neurocranium and LPJ, i.e., a true muscle sling.

From gross anatomical dissection it is not possible to determine exactly which components of the obliquus posterior muscle are incorporated into the compound muscle sling, and we have not undertaken an analysis of the ontogenetic transformations resulting in the compound muscle of pomacentrids. In view of this, the question of the homology of the resultant system with that of cichlids (Aerts, 1982; Claeys and Aerts, 1984), labrids and embiotocids (Liem, 1986; Liem and Sanderson, 1986) must remain open. The fact that a muscle sling is present only in some pomacentrid species poses problems for the analysis of this character at the level of the Labroidei.

Two possible interpretations suggest themselves based on this character distribution: 1) the pomacentrid muscle sling has been derived independently from that of the remaining labroids, or 2) a muscle sling is primitive for the Labroidei as a whole and has subsequently been lost within the Pomacentridae. Further information regarding the intrarelationships of the Pomacentridae may help resolve this question. For example, if the presence of a muscle sling within the Pomacentridae is found to characterize groups congruent with those characterized by other characters, a case could be made for suggesting the muscle sling developed within that clade. If, alternatively, the presence of a muscle sling is in conflict with the distribution of other characters and the absence characterizes corroborated groupings, absence could be considered as the derived condition. Lacking a precise knowledge of the intrarelationship of pomacentrid clades and based on the absence of a muscle sling in other pharyngognathous perciforms, we tentatively favor the second alternative and suggest that the muscle sling is indeed primitive for the Labroidei. However, we freely acknowledge that this is a relatively weak assumption and that future work may support alternative interpretations.

A remarkable similarity exists between the labroid muscle sling and that of exocoetid beloniforms (compare Figs. 2E and 9A or B). In the latter group the le4 (and a small slip of the levator posterior muscle) merges with a division of the obliquus posterior and inserts onto the LPJ, thus morphologically (and presumably also functionally) simulating the labroid configuration in remarkable detail. A similar muscle sling is not developed in the scomberesocids (Fig. 2D), and in these taxa a well-developed obliquus posterior and a fifth adductor connect the LPJ with the dorsal elements. The le4 and levator posterior both insert onto the head of the fourth epibranchial, and no fibers pass below it.

Quite apart from the striking suite of (homoplastic) morphological similarities

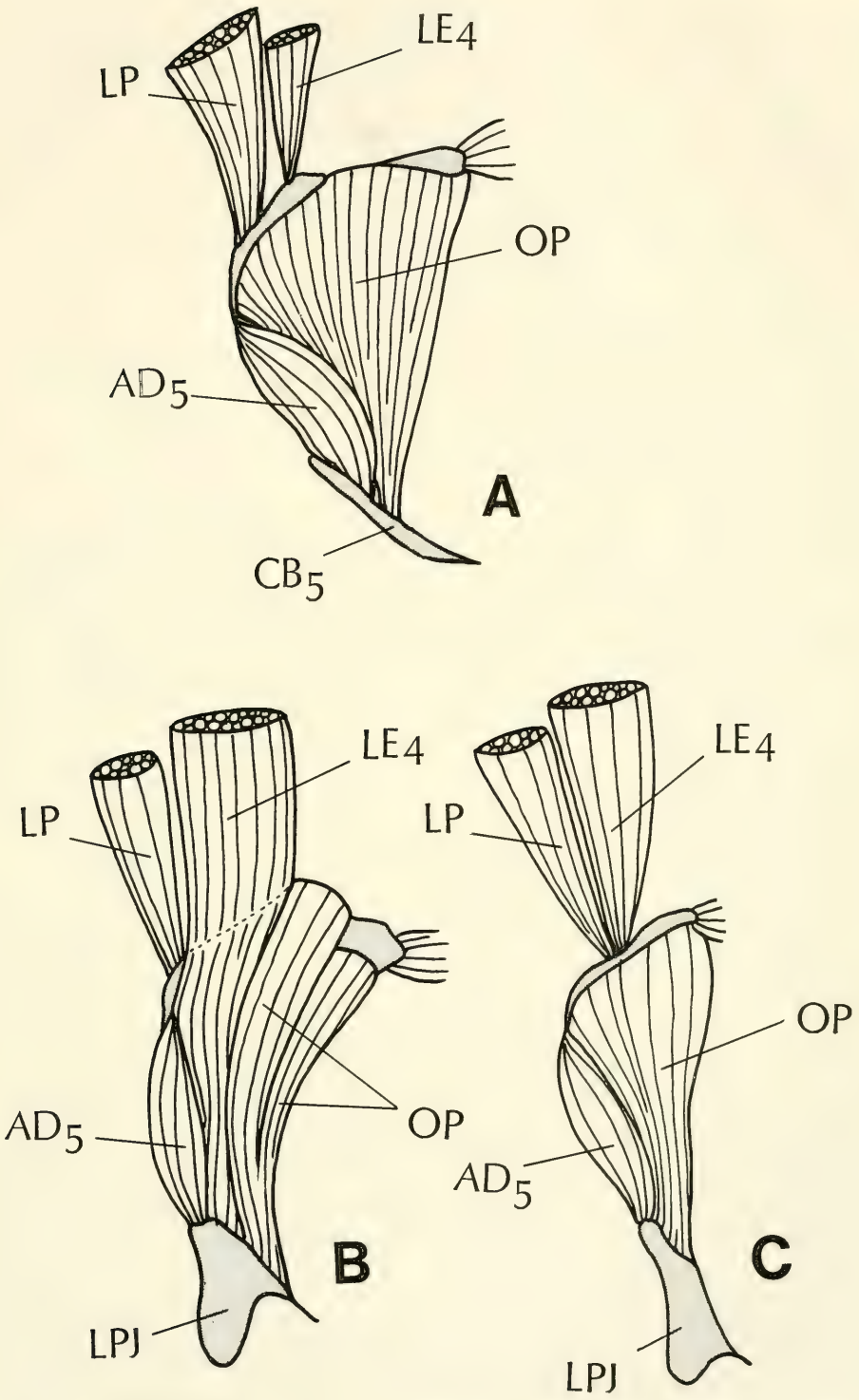

Figure 8. Isolated pharyngeal "muscle sling" components in: A. *Percichthys*; B. *Stegastes*; C. *Chromis*.

between the PJAs of exocoetids and labroids, these two lineages (as well as the scomberesocids) differ from other taxa in that *all* members possess the pharyngognathous condition of functionally united fifth ceratobranchials, regardless of the diet of each species. In other families the expression of pharyngognathy is limited to only a few (presumably duraphagous) members of each lineage, and is repeatedly correlated with an overall pharyngeal hypertrophy. The labroid pharyngeal synapomorphies (and the similar, but independently derived, beloniform ones) are not simply correlated with a durophagous diet; these taxa bear the synapomorphies regardless of the particulars of diet and trophic modification peculiar to individual species.

As indicated by the above discussion, the possession of united fifth ceratobranchials, i.e., pharyngognathy, is actually quite mosaically distributed among perciforms and at this level at least, is not indicative of any close phylogenetic relationship between the taxa in which it occurs. Thus, although it was originally in this context that the taxa comprising the Labroidei were considered to be closely related, the shared possession of the pharyngognathous condition is not itself the most compelling evidence for the monophyly of this clade. However, the fact that *all* labroid taxa, with the exception of *Cichla* (Stiassny, 1982), express united fifth ceratobranchials does suggest that this feature may have some value in uniting the Labroidei. While it is true that most labroids have a hypertrophied PJA capable of a powerful pharyngeal bite (Liem and Greenwood, 1981), this is by no means universal within the clade (e.g., Emery, 1973; Stiassny, 1982; Yamaoka, 1978). Nevertheless, even those labroids with extremely weak pharyngeal development exhibit the pharyngognathous condition of fused fifth ceratobranchials. Such universality of pharyngognathy, in the face of considerable pharyngeal variation, is unique among perciforms, and we consider this to be an indication that structural and functional union of the fifth ceratobranchials is primitive for the Labroidei and that its presence in forms with poor pharyngeal development merely reflects a retention of the primitive condition.

The Labroidei can thus be diagnosed on the basis of the presence of the following configuration of the pharyngeal jaw apparatus:

1. A LPJ with a well-developed ventral keel, onto which is inserted a portion of the transversus ventralis IV muscle.
2. A true diarthrosis between the UPJ and neurocranial apophysis.
3. A neurocranial apophysis of characteristic ventrally projecting and rounded form.
4. Presence of a m. transversus pharyngobranchialis 2 division of the transversus anterior muscle complex (secondarily reduced in the Embiotocidae). This character is somewhat ambiguous (see discussion on page 276).
5. An undivided sphincter oesophagi muscle.
6. A muscle sling directly suspending the LPJ from the neurocranium (polymorphically expressed within the Pomacentridae). See page 284 for a discussion of this character.
7. A structural union of the LPJ even in the absence of pharyngeal hypertrophy and functional duraphagy.

The interesting preponderance of characters concerning the pharyngeal jaw apparatus in labroid systematics is discussed further on pages 306–308. In the course of this investigation a further character of the pharyngeal region (although not obviously functionally related to the PJA) has been identified, and before concluding this section on labroid monophyly that character is discussed.

As already noted, extensive data exist on the configuration of dorsal branchial arch elements in acanthomorph fishes, but considerably less is known about variation in the ventral branchial elements. Fortu-

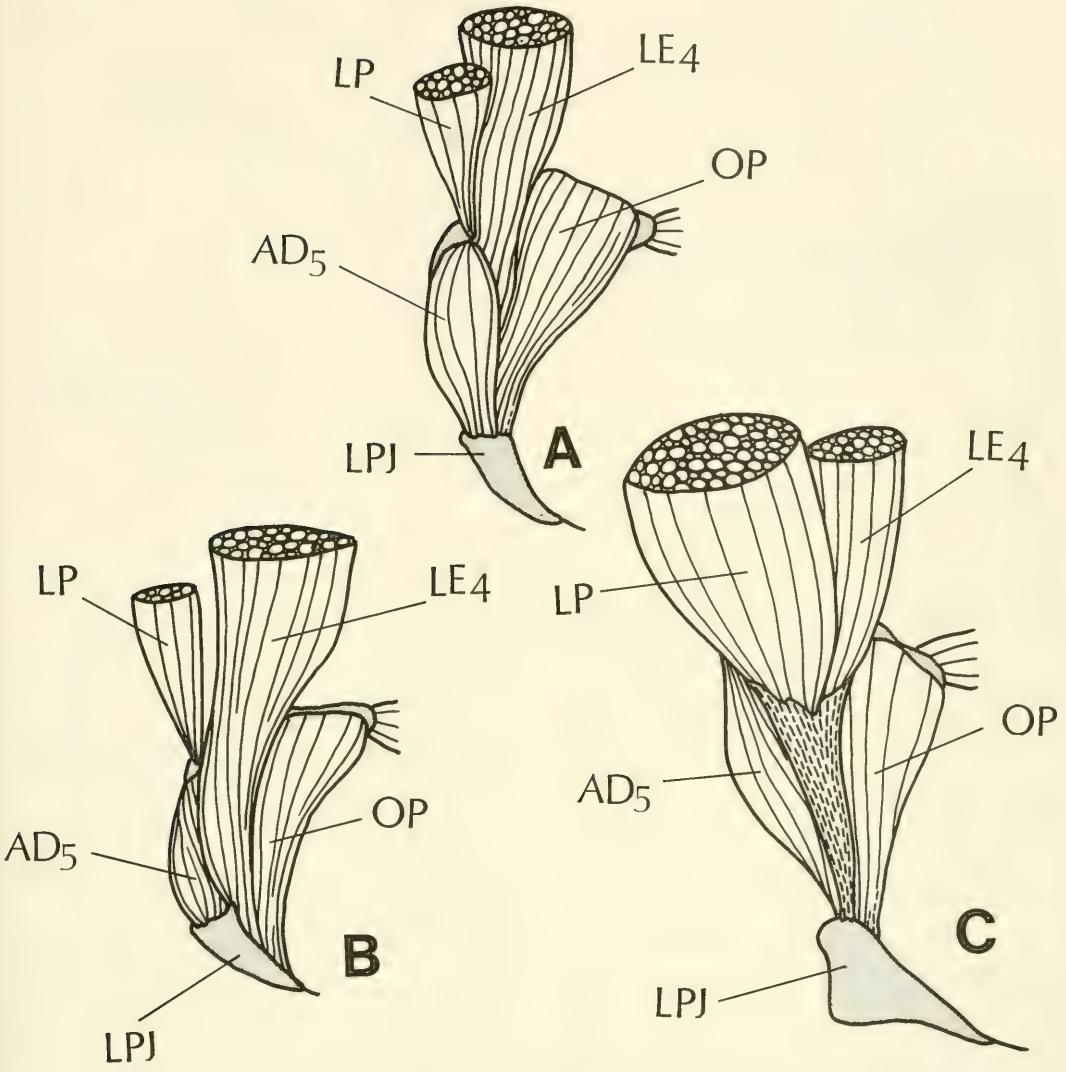

Figure 9. Isolated pharyngeal "muscle sling" components in: A. *Astatotilapia*; B. *Ditrema*; C. *Labrus*.

nately some comparative data are available (e.g., Nelson, 1967a, 1969; Travers, 1984a,b). Investigation of the configuration and associations of the ventral branchial arch elements of labroid fishes renders several features that may be potentially useful in resolving labroid intrarelationships (page 296).

In addition to these features, a particular configuration of basibranchial elements characterizes the entire Labroidei. In labroids the first basibranchial is an elongate, cylindrical element situated partially below the axis of the basihyal and the remaining elements of the basibranchial series (Figs. 10A–E). Although there is considerable variation in this osteological complex, the first basibranchial does not lie below the axis of the basihyal and remaining elements in the majority of outgroup taxa examined. In most outgroup taxa, rather, the first basibranchial is a lat-

erally compressed, almost square element and the basihyal/basibranchial series are more or less horizontally aligned with the first basibranchial abutting the caudal margin of the basihyal element (Fig. 10D; Nelson, 1967a, 1969; Travers, 1984a,b). Among outgroups a similar configuration was found only in the girellid, *Girella*.

In view of its limited distribution, *the presence of an elongate, cylindrical first basibranchial element ventrorostrally displaced to lie partially below the basihyal axis is interpreted as an additional synapomorphy uniting the labroid clade*, and the presence of similar modifications in *Girella* is presumed to be homoplasous.

In summary, the monophyly of the Labroidei seems to have been established beyond any reasonable doubt. Seven of the eight characters used in the definition of the assemblage are features of the pharyngeal jaw apparatus, and the eighth (i.e., the basibranchial character described above), although not obviously implicated in the PJA, is also a character of the pharyngeal region. Despite a conscious and concerted effort to locate synapomorphies in other structural (functional) systems, the weight of evidence for labroid monophyly remains in the pharynx (see discussion on pages 306–308).

LABROID INTRARELATIONSHIPS

Character Survey

In this section we review the various characters that have been used in previous analyses of labroid intrarelationships, and present novel data. For ease of description, the characters are arranged into rather loosely defined morphological units wherever possible; otherwise they are simply listed independently. Where appropriate each character or character complex is introduced with a short review of the relevant comparative literature and any problems surrounding past usage of terms or identification of homologies are discussed. As in the preceding section, summary statements of characters assessed to be synapomorphic for labroid clades are italicized for ease of reference.

Characters of the Pharyngeal Jaw Apparatus

LPJ Union and Medial Tooth Implantation. As we mentioned, within the Labroidei two modes of LPJ union are expressed. In cichlids the two fifth ceratobranchial elements are united medially in a caudally convoluted and interdigitating suture (Fig. 3B), and the pharyngeal teeth on the corresponding toothplate can be divided into left and right regions with no teeth located over the symphysis of the two bones. Regarding the retention of a sutural union, and the tooth implantation pattern, we agree with Kaufman and Liem (1982) that the cichlid arrangement represents the plesiomorphic labroid condition. In contrast, the condition in adult labrids, pomacentrids and embiotocids is a complete fusion of the two LPJ elements and no trace of the central suture remains (Figs. 3A, C, D). Tooth rows are arranged radially across the LPJ, and teeth are located over the median region of the jaw (Kaufman and Liem, 1982).

Because a similarly derived arrangement is found nowhere else among pharyngognath percomorphs, contrary to Kaufman and Liem (1982), we interpret *the total obliteration of all traces of a sutural union of the two fifth ceratobranchial elements of the LPJ and the implantation of pharyngeal teeth over the midline of the bone to be synapomorphies uniting the labrid embiotocid and pomacentrid radiations.*

Pharyngo-Cleithral Joint. Liem and Greenwood (1981), and later Kaufman and Liem (1982) described what they termed "pharyngo-cleithral joints" in labrid and pomacentrid taxa. The latter authors were of the opinion that the joints in these two lineages are "clearly dissimilar in form" but offer little in the way of substantiation of the claim. The pharyngo-cleithral joint is listed as one of the synapomorphies

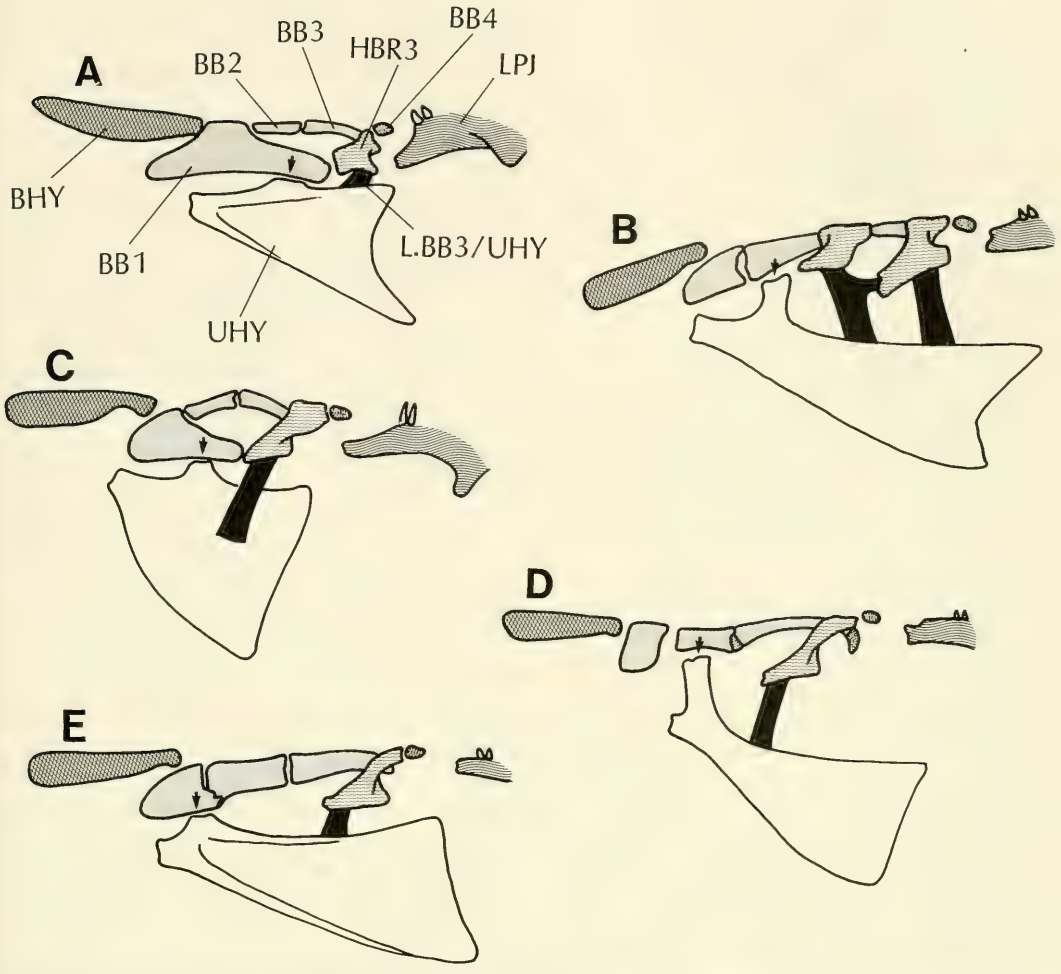

Figure 10. Ventral branchial arch elements in: A. *Labrus*; B. *Astatotilapia*; C. *Pomacentrus*; D. *Percichthys*; E. *Embiotoca* in lateral view.

characterizing the Labridae (Kaufman and Liem, 1982: 9), and Liem and Sanderson (1986) investigated the function of the joint during pharyngeal mastication. Lauder and Liem (1983: 169) cited the presence of a "pharyngo-cleithral articulation of characteristic form" as a synapomorphy of the Pomacentridae. Our observations of the pharyngeal-cleithral associations in various pomacentrid (Fig. 11A) and labrid (Figs. 11B, C) taxa are somewhat at odds with those of these previous investigators and lead to a different conclusion regarding the phylogenetic significance of the structural complex.

Among pomacentrids there is considerable variation in the degree to which the expanded lateral horn of the LPJ (=muscular process of Liem, 1973) contacts the cleithrum. In some taxa (e.g., species of *Microspathodon* and *Chromis*) there is no contact and a pharyngo-cleithral articulation is consequently lacking. In others (e.g., species of *Stegastes* and *Pomacentrus*) the area of contact is extensive and similar to that of many labrids.

Among labrids also there is considerable variation in the degree of pharyngo-cleithral contact and, although contact is always established (even in those forms with greatly reduced PJAs), the actual articulation surface may be extremely small (e.g., Fig. 11C). A distinct articular process (fossa?) on the cleithrum, and the consequent development of a true synovial joint (Liem and Greenwood, 1981) are not present in all labrids; in fact the development of such a joint appears to be present only in scarids and odacids (Kaufman and Liem, 1982: fig. 6). In our opinion the morphological differences between labrid (possibly excluding scarids and odacids) and pomacentrid pharyngo-cleithral articulations are quantitative and not qualitative as implied by Kaufman and Liem (1982). What is strikingly similar in these two taxa, however, is the form of the LPJ.

LPJ Form. Representative labroid LPJs are illustrated in Figure 3. Within each of the labroid families there exists a considerable range in both the relative size and shape of the LPJ. This is perhaps least marked in pomacentrids (Emery, 1973) and embiotocids (De Martini, 1969), but in labrids (Gomon and Paxton, 1986; Yamaoka, 1978) and cichlids (Fryer and Iles, 1972; Pellegrin, 1903) the range is truly remarkable. Despite intralineal variation and a number of autapomorphic features (Stiassny, 1980), the labrid and pomacentrid LPJs all share a markedly similar facies. These similarities are rather difficult to quantify precisely; however, they are easily appreciated by a comparison of each of the jaws illustrated in Figure 3. *The labrid/pomacentrid jaw is highly characteristic in being almost Y-shaped, rather than essentially triangular, with an emphasis upon the long lateral horns that are distally expanded. Uniquely in labrids and pomacentrids, LPJ width is greater than (rarely equal to) the LPJ length; this relation is reversed in other taxa. The elongation of the LPJ lateral horns and their distal expansion are synapomorphic features of the labrid and pomacentrid LPJ*; they are also a structural prerequisite for the development of a pharyngo-cleithral association. As pointed out above, although not strictly a character for use in our analysis, the development of a pharyngo-cleithral articulation in labrids, and its tendency for expression in the pomacentrids, is clearly correlated with these LPJ specializations.

LPJ Muscle Sling. Liem and Greenwood (1981) distinguished between a cichlid/embiotocid type of muscle sling on the one hand and a labrid type on the other. In the former, the fourth levator externus muscle is morphologically and functionally dominant during pharyngeal mastication, while in the Labridae it is the levator posterior muscle that is the dominant element (see also Liem, 1986; Liem and Sanderson, 1986; Yamaoka, 1978). Dominance of the fourth levator is considered by Liem and Greenwood (1981) to be part of an unique, specialized complex characterizing the Cichlidae-Embiotocidae lineage, while dominance of the levator posterior, forming a force couple with the pharyngocleithralis externus muscle, is considered by Kaufman and Liem (1982) to be one of the synapomorphies characterizing the Labridae.

It seems most probable that a structural and functional dominance of the fourth levator is the primitive condition of the labroid muscle sling for two reasons: in Pomacentrids the levator posterior never contributes to the muscle sling, and in outgroup taxa the levator posterior is invariably smaller and less well-developed than the fourth levator externus. The highly complex and elaborate muscular sling of the Labridae (Kaufman and Liem, 1982; Liem and Sanderson, 1986) is correctly interpreted as an autapomorphy of that clade.

Stiassny (1980) proposed that a caudad migration of the levator posterior origin away from the "lateral awning" (Barel *et al.*, 1976) on the ventral face of the pterotic or intercalar bone is a synapomorphy uniting the Embiotocidae and Labridae.

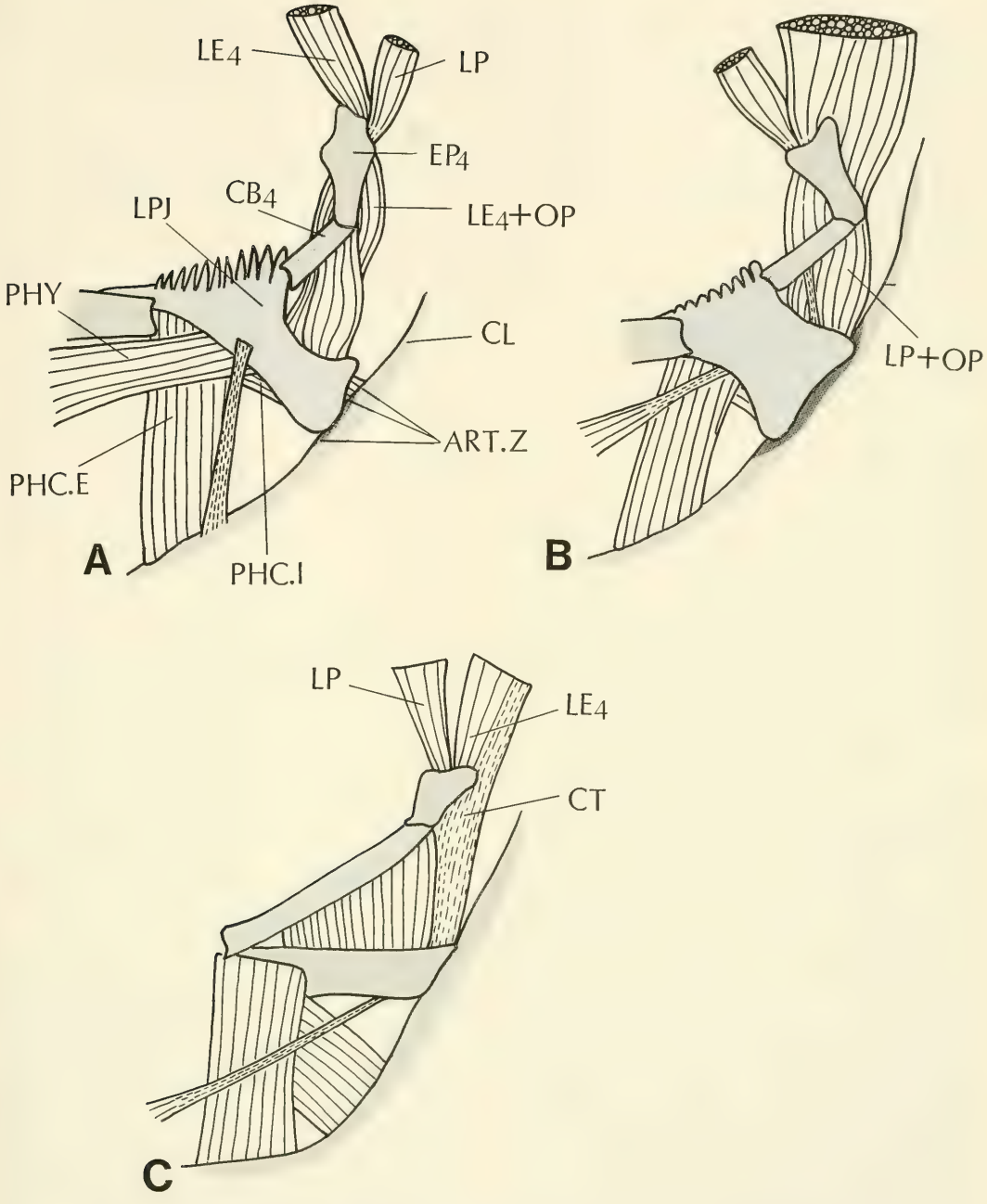

Figure 11. Pharyngo-cleithral associations in: A. *Eupomacentrus*; B. *Labrus*; C. *Labroides dimidiatus*.

Our reinvestigation of this character fails to reveal any significant differences between the location of levator insertion sites in pomacentrids, cichlids and embiotocids. Within the Labridae an extremely wide range of sites are encountered and based upon these Yamaoka (1978) has constructed a morpho-ecological classification of labrid types.

UPJ Composition. The structure of the dorsal gill arches has figured prominently in studies of euteleostean relationships (e.g., Nelson, 1969; Rosen, 1973), and a number of dorsal gill arch characters have direct bearing on relationships within the Labroidei (Kaufman and Liem, 1982; Liem and Greenwood, 1981; Nelson, 1967a; Stiassny, 1980, 1981). A summary of plesiomorphous osteological and myological features of the perciform upper pharynx is given by Stiassny (1981, 1982).

Upper Pharyngeal Toothplates. Compared with the modal perciform arrangement (Stiassny, 1981), within the Labroidei reduction of a number of features of dorsal gill arch osteology is evident. *In the Embiotocidae (Figs. 12B, 13B) and Labridae (Fig. 12D) the second pharyngobranchial is reduced to a slender, rod-like element with no trace of a second pharyngobranchial toothplate* (Nelson, 1967a). This condition stands in contrast to that seen in the Cichlidae (Fig. 12A), the Pomacentridae (Fig. 12C), and the majority of outgroups, in which the second pharyngobranchials are robust elements each bearing a well-developed toothplate.

Loss of the second pharyngobranchial toothplates occurs elsewhere within the Percomorpha, most notably among the Blenniidae (Springer, 1968), in which the entire second pharyngobranchial is absent and only a single toothbearing element (pharyngobranchial 3 and 4?) is present. In a single mastacembelid lineage the second pharyngobranchial is reduced to a small cartilage (Travers, 1984b). Despite the occassional loss of the second pharyngobranchial toothplate elsewhere within the Percomorpha (Stiassny, 1981), we consider the absence of this structure in the Embiotocidae and Labridae to be evidence suggestive of a sistergroup relationship between them.

As in the Euteleostei generally, the paired third pharyngobranchial elements (and associated toothplates) comprise the major component of the upper pharyngeal jaw in labroids (Nelson, 1967a, 1969). In the Cichlidae (Fig. 12A) and Pomacentridae (Fig. 12C) the fourth upper toothplates also contribute significantly to the composition of the UPJ, and are suturally united to their respective third pharyngobranchials. Typically among outgroup taxa the fourth upper toothplate is well-developed and cups around a cartilaginous fourth pharyngobranchial, although rarely it is as intimately associated with the third pharyngobranchial or as highly ossified as in cichlids and pomacentrids (Stiassny, 1981).

In embiotocids Up4 is a fragile, weakly ossified element with feebly developed teeth and relatively little common border with its associated third pharyngobranchial (Fig. 12B). In the Labridae no evidence remains of an independent Up4 (Fig. 12D; see also Nelson, 1967a, 1969). *We consider the reduction of the Up4 element in the upper pharyngeal jaw to be a synapomorphy of these two labroid taxa.* Ontogenetic data may clarify the nature of the reduction of this character within the Labridae.

The families Cichlidae and Embiotocidae share a cartilaginous cap on the anterior border of the second epibranchial (Fig. 14) (Stiassny, 1981). However, reinvestigation of this character leads us to consider this condition non-homologous between the two families. Within the Cichlidae, the second epibranchials bear an expansion rostrally with a cartilaginous cap. This cartilaginous flange does not articulate with any other pharyngeal element, and extends forward into the buccal cavity forming the core of pharyngeal pad developed on the mouth roof (Trewavas, 1973). In addition, the head of the epi-

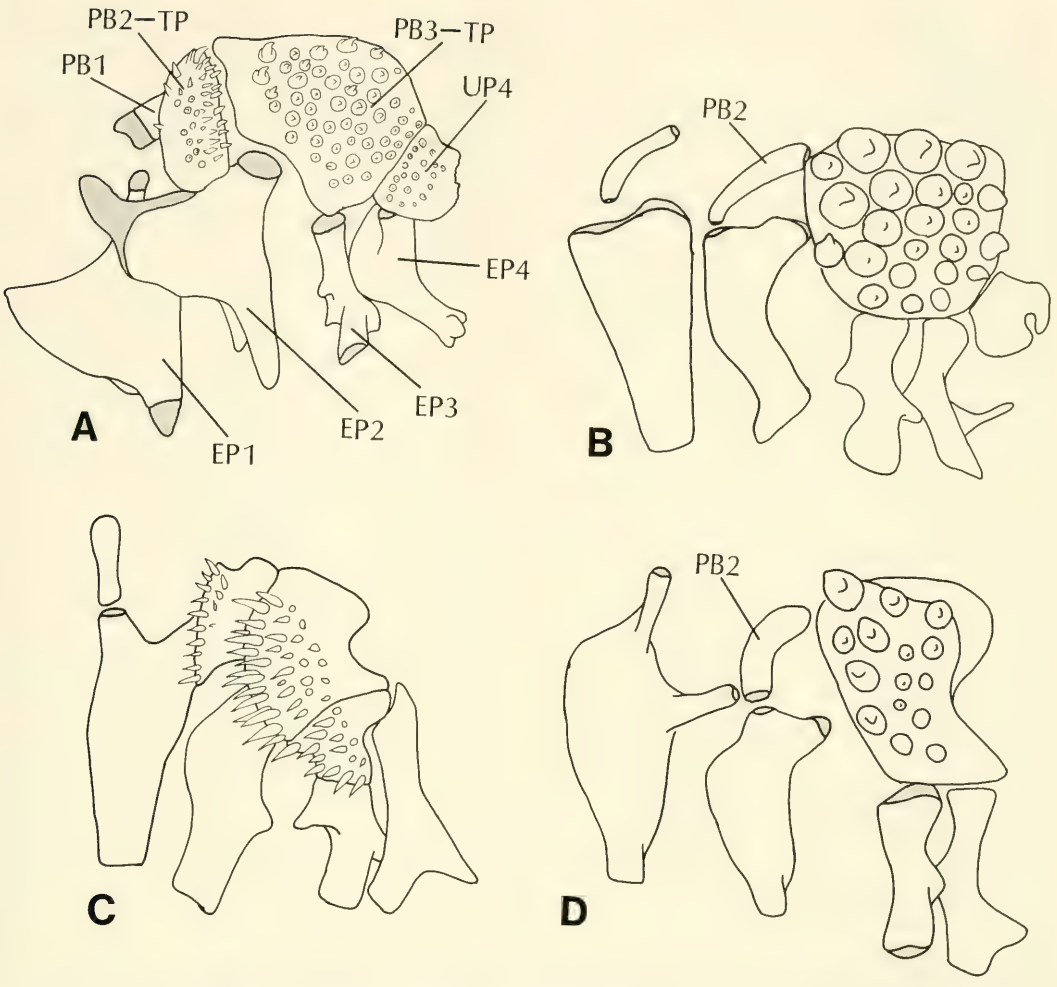

Figure 12. Right upper pharyngeal jaw in ventral view. A. *Geophagus*; B. *Micrometrus*; C. *Stegastes*; D. *Labrus*.

branchial bears two other cartilaginous pads, corresponding to its points of articulation with pharyngobranchials 2 and 3 (Fig. 14A). Within the Embiotocidae, only those cartilaginous pads associated with the pharyngobranchial articulations are present (Fig. 14B), either continuous with each other or separated by a narrow gap. Because the cartilaginous extension on the anterior border of the second epibranchial has no counterpart in the Embiotocidae, in terms of either form or topographic relationship to the adjacent elements, we do not consider this similarity to be indicative of a close relationship between the two families.

Interarcual Cartilage Development. The presence of a cylindrical rod-like interarcual cartilage connecting the uncinate process of the first epibranchial element with a dorsal process of the second pharyngobranchial is considered by Rosen and Greenwood (1976) to be a synapomorphy uniting the Perciformes. In a subsequent review of the morphology and distribution of this structure Travers (1981) concluded that an interarcual cartilage (of some form) is primitively present in a wide

range of ctenosquamate taxa (see also Rosen, 1985).

Among outgroup taxa investigated here a rod-like interarcual cartilage is typically present. Although a well-developed interarcual cartilage is present in most sciaenid and gerreid taxa examined, an interarcual cartilage is lacking in both pharyngognaths *Pogonias cromis* and *Gerres poeti*. Within the Perciformes the interarcual cartilage has apparently been lost independently a number of times (e.g., Springer, 1968; Travers 1981, 1984a). Johnson (1984) listed the presence or absence of an interarcual cartilage in representatives of all percoid families.

Within the Labroidei, a rod-like interarcual cartilage is fully developed in the Pomacentridae (Fig. 13C), reduced or absent among the Cichlidae (Fig. 13A; see also Stiassny, 1981), and completely absent in both the Labridae (Fig. 13D) and Embiotocidae (Fig. 13B). The cichlid condition is complex as an interarcual (present as a nubble of cartilage suspended in a connective tissue strand) occurs in many Neotropical and Madagascan lineages but is present only very rarely as an individual anomaly in the more derived African lineage (Stiassny, in press). As the Cichlidae is polymorphic for this character we tentatively consider the cartilage to be primitively present, but reduced in the family, perhaps having been lost independently several times within the clade. *The complete absence of an interarcual cartilage is interpreted as a synapomorphy of the Labridae and Embiotocidae.*

Stiassny (1980) cited the loss of a well-developed anterodorsal process on the second pharyngobranchial (primitively accommodating the medial end of the interarcual cartilage) as a synapomorphy uniting the Labridae, Embiotocidae and Cichlidae. Reexamination of this character fails to corroborate that assessment. Comparison of second pharyngobranchial morphology in a range of cichlid and pomacentrid and additional outgroup taxa does not reveal any significant difference in the degree of development of this process in these taxa. The fact that the process is lacking on the second pharyngobranchials of labrids and embiotocids is clearly related to the overall reduction of the elements in these taxa.

With regard to branchial osteology, the monotypic family Pholidichthyidae mirrors the Labridae (and in some respects other labroids also) to a remarkable extent. *Pholidichthys* lacks a cartilaginous fourth pharyngobranchial, a fourth upper toothplate, epibranchials 3 and 4 articulate with the third pharyngobranchial, no interarcual cartilage is present and the second pharyngobranchial lacks a toothplate and anterodorsal process (Springer and Freihofer, 1976). In addition the fifth ceratobranchials of *Pholidichthys* are also united into a single element. Unfortunately no specimens of this genus were available to us for dissection so we are unable to comment on the condition of the branchial myology of these fishes. An investigation of their myological configuration is particularly interesting with regard to the possible development of a pharyngeal muscle sling in these taxa. (See discussion of beloniform/labroid pharyngeal parallels on pages 274–286.)

Additional Characters of the Pharyngeal Region

Ventral Branchial Myology. In a phylogenetic context, teleostean ventral branchial myology has received far less attention than the corresponding dorsal configuration. Although much information is available in papers describing the myology of various individual taxa, few comparative data have been assembled with a view to resolving problems of phylogenetic relationship. The works of Dietz (1921), Nelson (1967b), Winterbottom (1974) and Lauder (1983) are notable exceptions and provided much valuable comparative information. Goedel (1974a,b) and Anker (1978) also provided useful data on the ventral branchial mus-

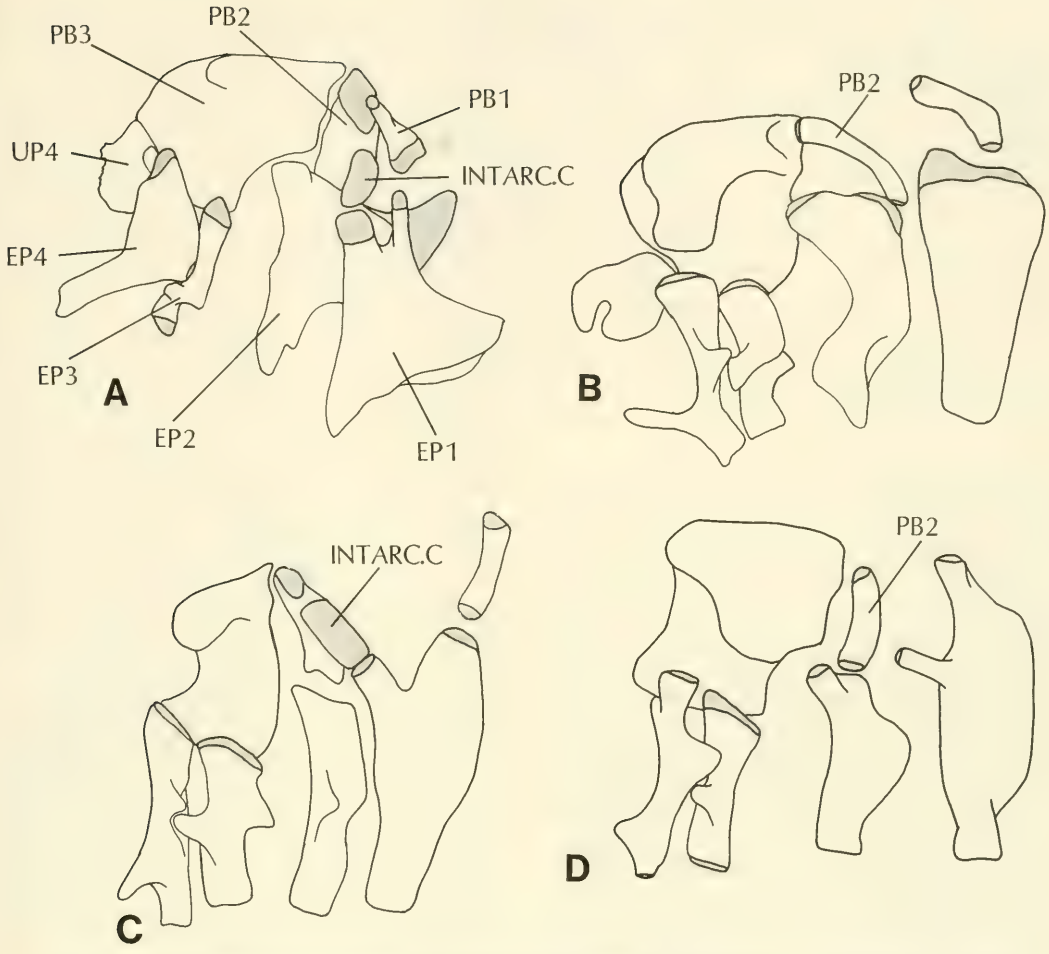

Figure 13. Right upper pharyngeal jaw in dorsal view. A. *Geophagus*; B. *Micrometrus*; C. *Stegastes*; D. *Labrus*.

cles of two African cichlid fishes, and characters of the ventral branchial musculature of labroids are employed by Stiassny (1982, and in press) and Greenwood (1985).

The plesiomorphic perciform configuration of ventral branchial muscles is represented here by the arrangement in *Morone* (Fig. 4A). Both the rectus ventralis IV and obliquus ventralis IV insert together onto a well-developed semicircular ligament system. Among labroids a similar configuration is present in embiotocids (Fig. 4B) and most cichlids (Fig. 4C; Greenwood, 1985 and Stiassny, in press), as well as in the percoid outgroups examined (*Serranus* lacks the semicircular ligament system entirely [Stiassny, in press]).

In labrids (Fig. 4D) and pomacentrids (Fig. 4E) the rectus IV and obliquus IV muscles insert independently on the semicircular ligament. Although a seemingly minor distinction, these insertional differences consistently appear to differentiate labrids and pomacentrids from the other perciform taxa examined, and as such are interpreted as synapomorphic for the two lineages.

Primitively among acanthomorphs a

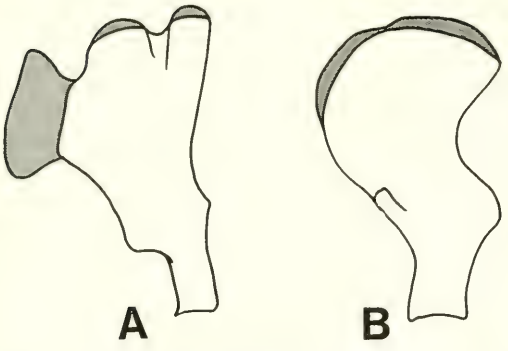

Figure 14. Isolated second epibranchial element. A. *Astatotilapia*; B. *Cymatogaster*.

single ligament passes from the third hypobranchial element of either side to attach to the dorsal surface of the urohyal (ligamentum urohyale caudale of Anker, 1978). Uniquely in the Cichlidae (Fig. 10B) an additional ligament (ligamentum urohyale intermedium of Anker, 1978) passes from the second hypobranchial element of either side to attach to the dorsal surface of the urohyal somewhat in advance of the caudal ligament. A similar elaboration of a ventral branchial ligament system is lacking in all other taxa and is identified as an additional synapomorphy uniting the members of the Cichlidae.

Ventral Branchial Osteology. There exists a large body of data on the configuration of dorsal branchial osteology, but as with the myology of the region, less is known of the variation in the ventral branchial elements. Some comparative data are available (e.g., Nelson, 1967a, 1969; Travers, 1984a,b) and these provide useful additional outgroup data.

In labrid (Fig. 10A), pomacentrid (Fig. 10C) and embiotocid (Fig. 10E) taxa the urohyal articulates via its dorsal process with the ventral surface of the first basibranchial element. This is not the case in cichlids (Fig. 10B), nor in the majority of percoid outgroups examined (e.g., Fig. 10D) where the urohyal articulates with the second basibranchial (occasionally at the cartilaginous junction of the first and second basibranchials).

Gerres and *Eucinostomus* provide exceptions to the above generalization and in these taxa the urohyal (although lacking a distinct dorsal process) articulates directly with basibranchial one. A similar association is present in the majority of Asian (but not African) mastacembelids and synbranchids (Travers, 1984a,b).

Despite these few mosaic occurrences, in the overwhelming majority of acanthomorph taxa the urohyal articulates with the second basibranchial, and the occurrence of *a basibranchial one/urohyal association in labrids, pomacentrids and embiotocids is interpreted as a synapomorphy uniting these three taxa.*

In labrids and pomacentrids (Figs. 10A, C) the urohyal articulates with a large keel-like caudally directed ventral extension developed on the elongate cylindrical first basibranchial element. Primitively among perciforms the first basibranchial is a deep, almost square element that lacks a ventral process (e.g., Fig. 10D). In cichlids and embiotocids the first basibranchial is also somewhat elongate and cylindrical and varies in size. A well-developed caudally directed ventral process, however, is never developed in the manner or extent approaching that of the pomacentrids and labrids.

The mastacembelid and synbranchid lineage described by Travers (1984a,b) prove exceptional among outgroups in the possession of well-developed ventral processes on the first basibranchial.

Despite the occurrence of a similar basibranchial morphology in the labrid/pomacentrid pair and in the distantly related symbranchid/mastacembelid lineage, the labrid/pomacentrid basibranchial configuration is interpreted as a synapomorphy uniting these two taxa.

Caudal Fin Skeleton. Extensive literature exists on the systematic value and distribution of variation in caudal structure within the Acanthomorpha (e.g., Ford, 1937; Gosline, 1961; Hollister, 1936, 1937;

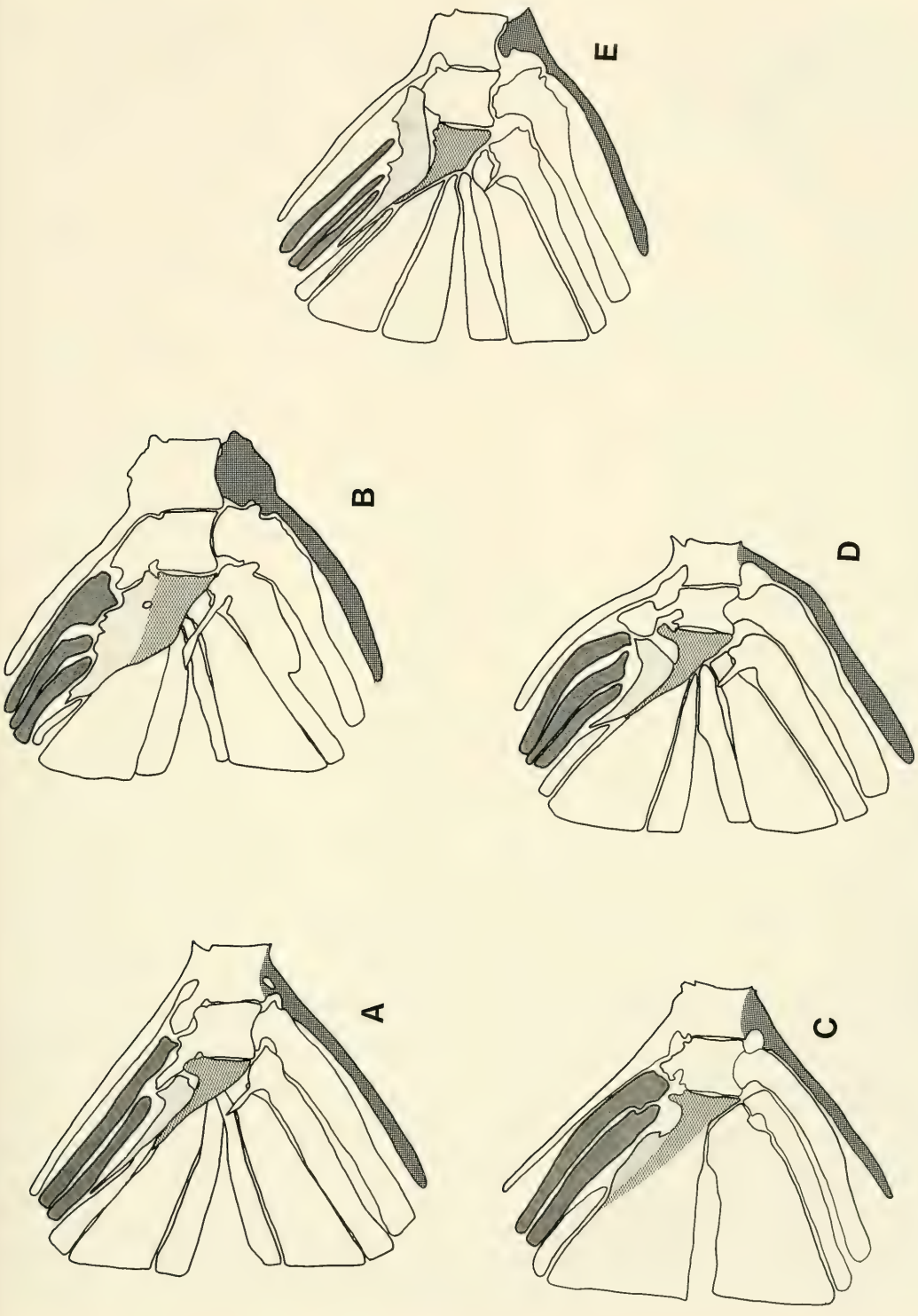

Figure 15. Caudal skeleton of: A. *Cichla*; B. *Stegastes*; C. *Labrus*; D. *Embiotoca*; E. *Percichthys*.

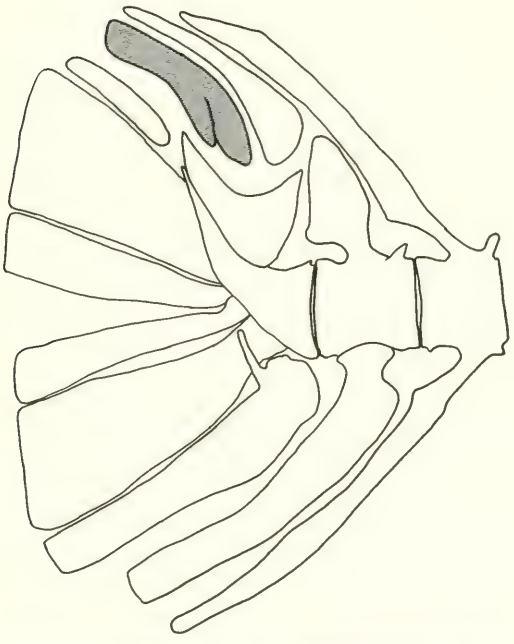

Figure 16. Caudal skeleton of A. *Hysterocarpus* (40 mm SL).

Johnson, 1984; Patterson, 1968; Rosen, 1973; Rosen and Patterson, 1969). The basal perciform caudal skeleton has been described by Gosline (1961) as having three epurals, two independent uroneural ossifications, and the hemal arches on the penultimate and antepenultimate vertebrae autogenous. Patterson (1968) further characterized the basal Perciform caudal skeleton as having, among other features, a low neural crest on the penultimate vertebrae.

Epural Reduction. In labrid (Fig. 15C; see also Ford, 1937) and cichlid (Fig. 15A; see also Vandewalle, 1973) taxa there are two epural bones in the caudal skeleton. Among perciforms the primitive condition, as found in the Embiotocidae (Fig. 15D), Pomacentridae (Fig. 15B), and most of the outgroup taxa examined (e.g., Fig. 15E), is the possession of three epurals (see also Gosline, 1961). Although exceptional among embiotocids, individuals of *Hysterocarpus* (Fig. 16) and *Micrometrus* are occasionally found with only two independent epurals. In these individuals the anomaly appears to be the result of fusion. In young *Hysterocarpus,* three separate epurals are present, whereas in the adult these are occasionally united along a portion of their border. The labrids and cichlids bear no trace of a third epural at any time during ontogeny.

Despite the somewhat mosaic distribution of epural reduction among phylogenetically disparate acanthomorph taxa (e.g., reduction occurs in a range of serranid lineages as well as in a number of "paracanthopterygians" [Rosen and Patterson, 1969]), three epurals is undoubtedly the primitive condition for percomorphs (Patterson, 1968). In view of this *we interpret the reduction of epural number in the Labridae and Cichlidae as a synapomorphy uniting the two clades.*

Uroneural Ossification. In common with a range of perciform taxa, the labroid caudal skeleton has but a single uroneural ossification (Gosline, 1961). In the Embiotocidae and Cichlidae, the uroneural is autogenous, as it is in all outgroup taxa examined (e.g., Fig. 15E). Embiotocids differ from outgroups, however, in having the uroneural elements very closely applied to the urostyle (Fig. 15D); nonetheless the uroneural can easily be dissected free of the urostyle without damage to either element. In the Pomacentridae and Labridae the uroneural element is completely fused with the urostyle, resulting in a urostyle/uroneural block with no suture evident between the two elements (e.g., Fig. 15B). In labrids, hypurals 4 and 5 are also fused to the uroneural/urostyle block (Fig. 15C; see also Ford, 1937), a condition we consider to be synapomorphic for members of the Labridae.

Complete fusion of the uroneural with the urostyle, and the obliteration of all trace of a former sutural union, is interpreted as a synapomorphy uniting the pomacentrid and labrid clades.

Antepenultimate Vertebrae. Primitively among perciforms, the hemal arch of

the antepenultimate vertebra remains free from, although very closely associated with, its centrum (e.g., Fig. 15E; see also Gosline, 1961). Among labroids an autogenous hemal arch is also found in the Pomacentridae (Fig. 15B), where the hemal spine of the antepenultimate vertebra articulates with the centrum via a peg-like dorsal extension. The division between the two bones is clearly evident. Embiotocids, cichlids, and labrids exhibit a derived condition in having the hemal spine fused with the antepenultimate vertebra. Even in the early ontogeny of these elements (ca. 10 mm SL), there is no discernible division between these elements.

Although fusion of the antepenultimate centrum and hemal spine occurs in some other acanthomorph taxa (e.g., Gosline, 1961; Hollister, 1937; Springer, 1968), its absence in any of the perciform outgroup taxa examined in the course of our investigation leads us to consider this character as a synapomorphy uniting the labrids, embiotocids and cichlids.

Additional Characters

Subocular Shelf. The presence of a subocular shelf, usually formed by a medial extension of the third suborbital, is widespread among perciforms and appears to have been independently lost a number of times within this taxon (Smith and Bailey, 1962). Among the labroids the Pomacentridae and Embiotocidae have the subocular shelf, whereas the Cichlidae and Labridae do not. The markedly mosaic distribution of this character among outgroups renders polarity determination of the character extremely difficult. For example, a subocular shelf is absent in the Centrarchidae, Kyphosidae, Leiognathidae and Percidae, but is present in the Girellidae, Serranidae, and Sparidae. Even within the Gerreidae, this character is variable (Smith and Bailey, 1962). Clearly the subocular shelf has been lost repeatedly during perciform evolution. In the absence of a clearer knowledge of the precise relationships of the labroids to other perciform taxa, we are unable to determine the primitive labroid condition.

Endopterygoid Shelf. As noted by Stiassny (1980), primitively among acanthomorphs, the endopterygoid bone of the suspensorium bears a medially directed shelf forming the floor of the orbit. The adductor arcus palatini muscle inserts onto the endopterygoid shelf and, although the extent of adductor migration over the shelf varies (Rosen, 1973), insertion is invariably onto the lateral face of the bone.

In labrids and cichlids the medially directed endopterygoid shelf of other acanthomorphs is lacking, and the adductor arcus palantini inserts onto the medial face of the endopterygoid. The floor of the orbit now lacks a bony component and is instead entirely muscular. In both pomacentrids and embiotocids the endopterygoid shelf is well-developed and adductor insertion is onto its medial face.

Among all of the outgroup taxa investigated an endopterygoid shelf was lacking only in the single species of Mullidae examined. In this taxon the adductor also inserts onto the medial face of the bone and the floor of the orbit is entirely muscular. *In view of the extremely limited distribution of this feature within the Acanthomorpha, we interpret the loss of an endopterygoid shelf, and the subsequent migration of the adductor arcus palatini muscle from the lateral to the medial face of the endopterygoid, to be a synapomorphy of the Cichlidae and Labridae.*

Predorsal Bones. The structure and evolution of the predorsal bones have been extensively reviewed by Smith and Bailey (1961). Predorsals have generally been viewed as representing rayless pterygiophores (Smith and Bailey, 1961); however, it has recently been suggested that they are derived from neural arch material (P. Mabee, personal communication). Whatever their origin, variation in predorsal number is widespread and may be systematically useful at the present level of analysis.

The possession of three predorsal bones is the most common condition among the percoids (Johnson, 1984; Smith and Bailey, 1961) and, judging from the condition seen in most outgroup taxa, is primitive for the Labroidei as well.

Embiotocids and pomacentrids generally retain the primitive number of three predorsal ossifications, whereas the cichlids and labrids display a reduction in predorsal number. *The reduction in predorsal number, to two predorsals in the Labridae and to two or fewer in the Cichlidae, is considered to be a synapomorphy uniting these two families.*

Extrascapular Bones. Among percomorphs the extrascapular series of laterosensory canal bearing ossifications usually overlie the parietal region of the neurocranium. In those taxa in which the expaxial musculature has migrated onto the neurocranium the extrascapulars lie in the dermis superficial to the epaxial musculature (e.g, the Cichlidae). Uniquely among perciforms the extrascapulars have become fused with the parietals of embiotocids and pomacentrids. In these taxa the parietals each bear an open (or partially closed) tube running postero-laterally from the anterior parietal/supraoccipital border (Fig. 6C, D). *In agreement with Morris (1982) we consider the fusion of an extrascapular element with the parietal to be a synapomorphy uniting the Pomacentridae and Embiotocidae.* However, we are unable to corroborate Morris' assertion that a similar extrascapular/parietal fusion also characterizes the Scorpididae. In the representative scorpidid, kyphosid and girellid taxa investigated here, the extrascapular exhibited no particularly close association with the parietal bone of the neurocranium.

Epihemal Ribs. So-called epihemal ribs are developed in some or all representatives of the perciform families Embiotocidae, Pomacentridae, Cichlidae, Scorpididae, Girellidae, Chaetodontidae, Cirrhitidae, and Centrarchidae. Morris (1982) considered the presence of epihemal ribs as an indication that the pomacentrids (Fig. 17A) and embiotocids (Fig. 17B) bear a closer relationship to each other than either does to cichlids or labrids. However, a review of these structures indicates that the use of the term epihemal rib needs clarification because it describes two morphologically and developmentally distinct structures.

The epihemal ribs of pomacentrids (and scorpidids, girellids, chaetodontids and cirrhitids) are membranous ossifications extending into the horizontal septum between the epaxial and hypaxial musculature, and would thus appear to be modified intermuscular bones. The epihemals of embiotocids (and centrarchids, and a single cichlid species, *Geophagus surinamensis*) appear to be modified pleural ribs. We conclude that the epihemal ribs of embiotocids are distinct from those of pomacentrids, and that they in fact represent pleural ribs, for the following reasons: 1) The epihemal ribs of embiotocids do not extend into the horizontal septum, 2) they are preformed in cartilage as are pleural ribs (but not intermusculars, which are membrane bones and hence are no longer preformed in cartilage (Patterson, 1977)), and 3) the intermusculars and epihemals occur in overlapping series (Fig. 17B; contra Morris, 1982), indicating separate identity.

Although work in progress (Jensen) indicates that the arrangement of epihemal ribs may be informative at the intrafamilial level of analysis, lack of identity between pomacentrid and embiotocid epihemal ribs precludes support for Morris' (1982) statement of relationships based upon these structures. The morphological correspondence between the epihemal ribs of embiotocids and of the single species of cichlid fish is interesting; however, this similarity has little systematic significance.

Maxillary-Palatine Ligament. Stiassny (1980) described a ligament connecting the postmaxillary process of the maxilla with the palatine and ectopterygoid bones of

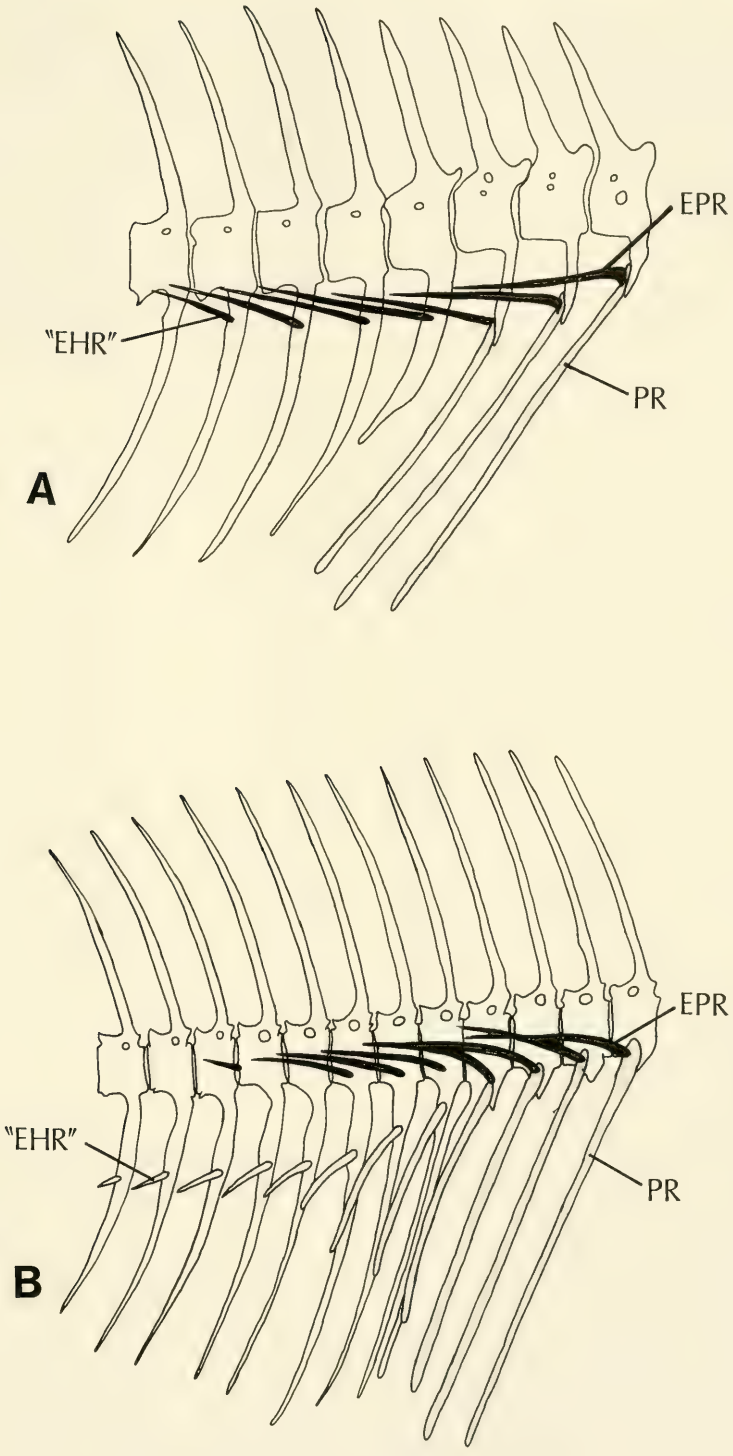

Figure 17. Epihemal ribs in: A. *Eupomacentrus*; B. *Embiotoca*.

the suspensorium as being a synapomorphy uniting the labrid and embiotocid lineages (see also Kaufman and Liem, 1982; Lauder and Liem, 1983). Our reinvestigation of this ligament fails to corroborate that assessment; the degree of development of the ligament varies markedly not only within other labroid taxa (e.g., a range of Neotropical and etropline Cichlidae possess a well-defined and discrete tract of connective tissue connecting the maxillae and palatine/pterygoid region), but also among a range of outgroup taxa examined during the course of this investigation. For this reason the presence of the ligament in labrids and pomacentrids is rejected as evidence of their close relationship.

tA_1 Insertion. Among percomorphs, and neoteleosts in general, control of the maxilla is achieved primarily through an insertion of the A_1 division of the adductor mandibulae muscle onto the posterior border of the maxillo-mandibular ligament, which runs from the lateral face of the maxilla to the lateral face of the angulo-articular (Rosen and Patterson, 1969; Stiassny, 1981). A tendon (tA_1) arising from A_1 and inserting onto the medial face of the maxilla is also primitively present, although usually only weakly developed. Within the Labroidei (and some percoids), there is no association of A_1 with the maxillo-mandibular ligament and maxillary control is primarily through tA_1 (Stiassny, 1980, 1981). The relative insertion sites of tA_1 in cichlids, embiotocids and labrids have been suggested to represent a morphocline of insertion from just below the cranial condyle (cichlids, Fig. 18C), to well onto the cranial condyle (in some embiotocids, Fig. 18A), to a point at the anterior margin of an elongate cranial condoyle (labrids, Fig. 18D). The insertion of tA_1 onto the cranial condyle was considered by Stiassny (1980) to be a synapomorphy of an embiotocid-labrid clade. Further investigation of this feature indicates that in fact this character exhibits a continuous range of variation both within and between taxa examined. For example, the embiotocids span a range of tA_1 insertions (Figs. 18A, B) from that found in cichlids and many other percoids to a condition approaching that of labrids. Within the Cichlidae, in addition, one occasionally finds a condition approaching that of the Labridae (e.g., in the etropline Cichlidae). In view of this, we feel that we would be creating an artificial discontinuity in what is in fact a continuous range of variation if we regarded tA_1 insertion as a synapomorphy of the Embiotocidae and Labridae.

Character Analysis

Figure 19 depicts the single minimum length tree derived by the PAUP branch and bound routine (Swofford, 1985). This is the shortest tree obtained from the character data (length = 23, consistency index = 0.652) and we favor it with due reservation. The resultant scheme of relationships differs from others previously proposed by Stiassny (1980), Liem and Greenwood (1981), and most recently by Kaufman and Liem (1982), in placing the Cichlidae as the sistergroup of all the remaining labroid groups. The integrity of a monophyletic assemblage composed of the Embiotocidae, Pomacentridae, and Labridae is supported by the presence of three uniquely derived features of the pharynx: the fifth ceratobranchial elements forming the LPJ are completely united such that no trace of a median suture remains, and the pharyngeal tooth rows span radially across the LPJ and overlie the median portion of the jaw (character 1 in Fig. 19); the urohyal articulates via its dorsal process with the first basibranchial element (character 2 in Fig. 19); and the musculus cranio-pharyngobranchialis 2 is absent (character 3 in Fig. 19). The Embiotocidae is placed as the sistergroup of the Pomacentridae plus the Labridae, again in contrast to previous hypotheses of other authors. Four pomacentrid/labrid synapomorphies are identified in a range of structural systems (characters 4, 5, 6, and 7 in Fig. 19).

Although Figure 19 represents the most

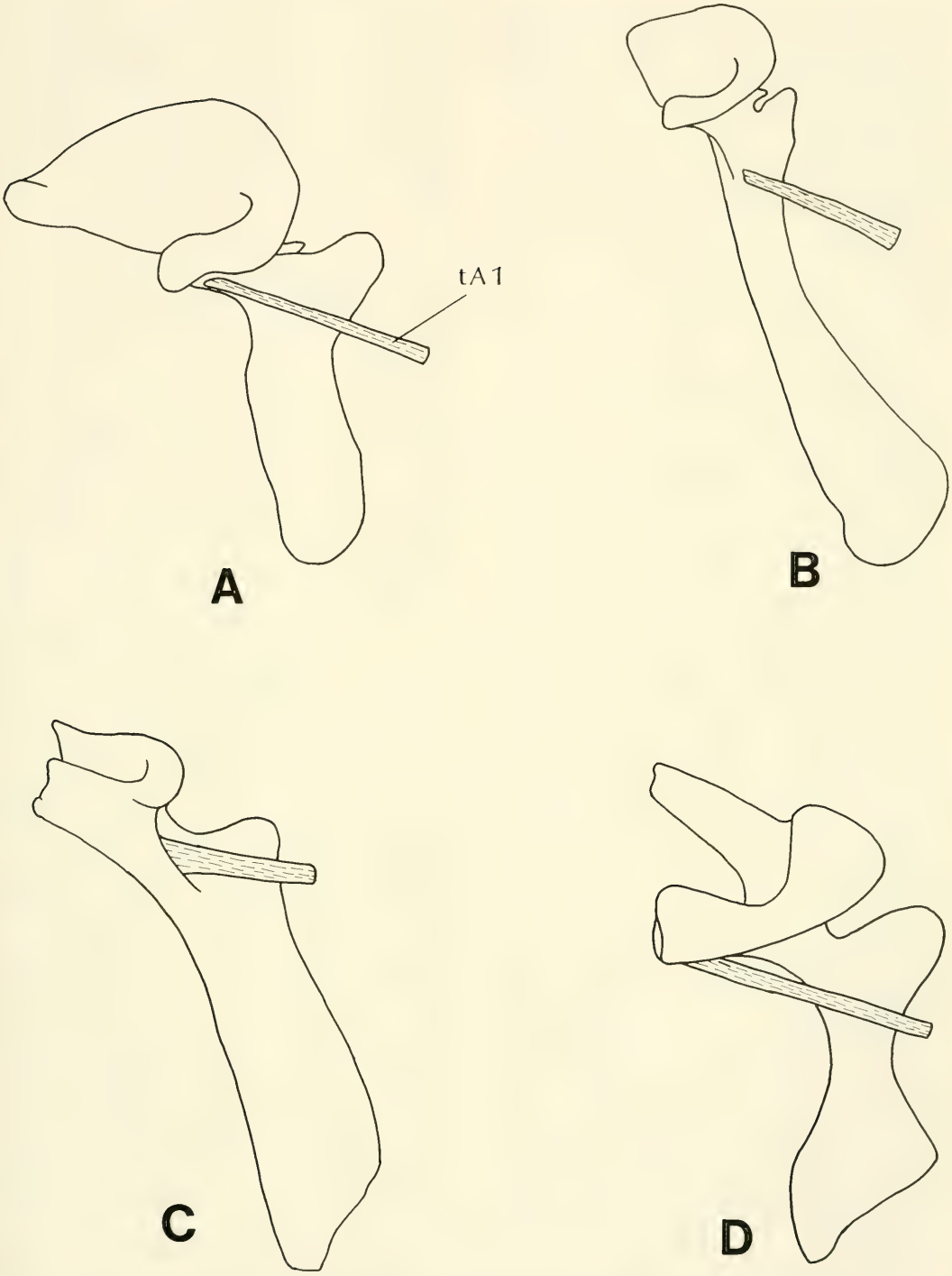

Figure 18. Insertion of tA_1 into the maxilla in: A. *Embiotoca*; B. *Hyperprosopon*; C. *Cichla*; D. *Labrus*.

parsimonious interpretation of the data at hand, the number of crossbars superimposed onto the cladogram starkly illustrates that even this scheme requires the loss or independent gain of many derived characters. Specifically, our hypothesis requires either that the Embiotocidae and Labridae have independently lost the second pharyngeal toothplates and reduced the pharyngobranchial element to a small rod-like structure (character 8), lost the interarcual cartilage (character 10), and have independently reduced (Embiotocidae) and lost (Labridae) the fourth upper toothplate (character 9), or alternatively that the Pomacentridae has undergone a reversal in each of these features. The Cichlidae and Labridae would have to have independently reduced the number of caudal epurals (character 11), reduced the number of predorsals (character 12), and developed an endopterygoid shelf with an (associated) shift in adductor arcus palatini muscle insertion site (character 13). The pomacentrids and embiotocids would have to have independently fused the second extrascapular bone with the parietal (character 14), or alternatively the Labridae would have to have secondarily re-expressed the ancestral condition of this character. Finally, the Pomacentridae would have to have redeveloped an autogenous antepenultimate hemal spine (character 15).

Obviously when dealing with such large amounts of homoplasy a number of alternative trees of nearly equivalent length can be computed. Figure 20 depicts all of the trees derived from our character data that are of length 27 or less. There is one tree of length 24 (1a in Fig. 20) and this, like our favored tree depicted in Figure 19, also places the Cichlidae as the sistergroup of the remaining Labroidei. Thus, the two shortest trees computed correspond in their placement of the Cichlidae, but differ as to which clade, the Embiotocidae or the Pomacentridae, forms the sistergroup of the Labridae. No trees of length 25 can be derived from these data. Diagrams 2a–f and 3a–b (Fig. 20) represent trees of lengths 26 and 27 respectively. Of the trees represented in Figure 20, only 2a has been previously proposed as a labroid phylogeny (Kaufman and Liem, 1982; Stiassny, 1980). There are two trees of length 29, including the tree of Liem and Greenwood (1981), and two trees of length 30.

Given the plethora of possible trees of nearly equivalent length and yet widely varying topologies, it is clear that statements of relationship within the Labroidei must remain highly tentative. For this reason it would be ill-advised to propose any classificatory or nomenclatural changes based upon the results of our study. Perhaps the most significant observation we can make is that morphological character transformations within the Labroidei display a disconcertingly large amount of homoplasy. No matter which scheme of relationship is ultimately chosen, we must accept and acknowledge that in many structurally (and functionally?) disparate systems, character distributions within the Labroidei present a perplexing "web of parallelism." As systematic morphologists we are obviously interested in knowing whether the degree of homoplasy revealed in our study of the Labroidei is a general phenomenon that will be observed repeatedly in different groups that are subject to such detailed morphological analysis, or if the magnitude of the problem is peculiar to this group—and is therefore perhaps indicative of something particular about its morphological evolution.

We hope that future work incorporating other types of data, for example cladistically analysed physiological or biochemical data (Wiley, 1981), will provide a set of characters more clearly supporting a single phylogeny. Once such a single, highly corroborated phylogeny is available, then the same morphological homoplasy that proved an impediment to our understanding of the relationships of the group suddenly becomes of great poten-

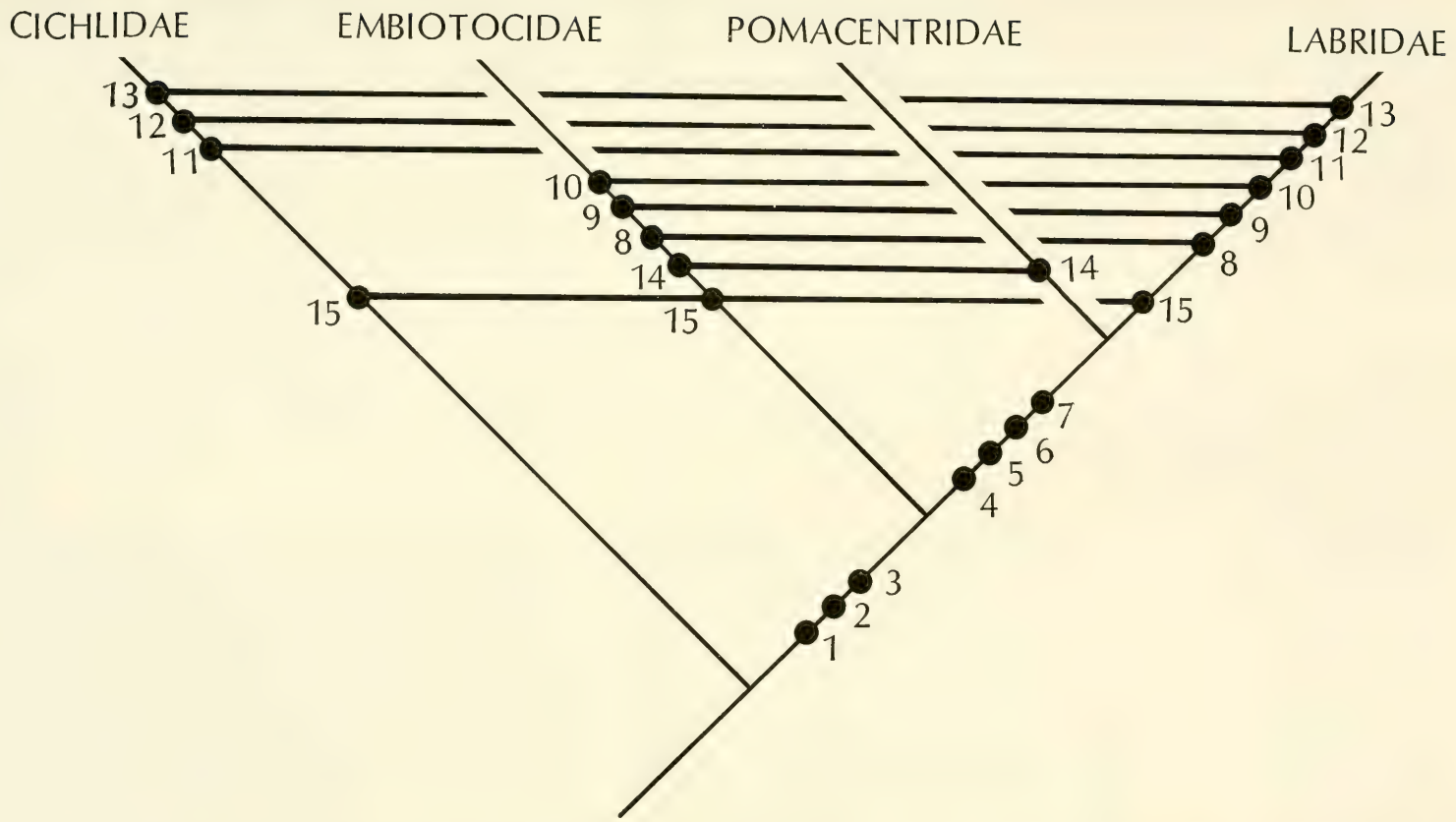

Figure 19. Cladogram of labroid relationships proposed in this study. Characters are: 1. LPJ with no trace of a central suture, and with pharyngeal teeth implanted directly over the midline. 2. Urohyal articulates with basibranchial one. 3. M. cranio-pharyngobranchialis 2 division of the transversus dorsalis muscle absent. 4. LPJ "Y-shaped" with short body and elongate lateral horns. 5. Obliquus ventralis IV and rectus ventralis V insert separately onto the semicircular ligament system. 6. Basibranchial one bears a large keel-like ventral extension. 7. Uroneural fused with the urostyle. 8. Second pharyngobranchial toothplate absent. 9. Fourth upper toothplate either markedly reduced or entirely lacking. 10. Interarcual cartilage absent. 11. Reduced number of caudal epurals. 12. Two of fewer predorsal bones. 13. Endopterygoid shelf absent and adductor arcus palatini inserts onto medial face of the suspensorium. 14. Extrascapular bone fused to the parietal. 15. Hemal arch of the antepenultimate caudal vertebra fused with the centrum.

tial use in extending our understanding of its evolution. Clades such as the Labroidei will provide an ideal opportunity for developmental genetecists, physiologists and morphologists to explore and elucidate the causal processes underlying morphological homoplasy.

DISCUSSION

Pharyngeal Complexity and Systematic Dominance

Of the eight characters found to diagnose the Labroidei, seven are elements of the PJA, and the eighth, although not obviously linked with the functioning of that apparatus, is a feature of the pharynx. Despite a conscious effort to locate additional synapomorphies in other structural systems we were able to find evidence of labroid monophyly only in the pharynx.

This predominance of PJA characters has not extended to our analysis of relationships within the Labroidei. Although features of the pharynx are well represented among the characters used, enough other characters from a reasonable "spread" of morphological systems are introduced so that pharyngeal information is not overwhelming at that level of analysis. Of the 15 characters used in the analysis of labroid intrarelationships (Figs. 19 and 20) only six are components of the PJA (characters 1, 3, 4, 8, 9 and 10). Three additional characters are located in the pharyngeal region but have no obvious functional connection with the PJA (characters 2, 5 and 6), and the remainder are distributed throughout the organism (characters 7, 11, 12, 13, 14 and 15). Despite the variety of sources of information regarding relationships within the Labroidei, we feel that the predominance of the pharynx as a source of information at the subordinal level is noteworthy and credits further consideration here.

When a particular morphological structure or functional complex plays such a disproportionately predominant role in the systematics of a group of organisms there are several reasons why that region or complex may be of interest. While freely acknowledging that many non-morphological features can be of equal, and sometimes even primary, importance in the evolution of groups and their interrelationships (Mayr, 1969; Miller, 1949), we will restrict ourselves to a consideration of the particular morphological properties of groups:

1. The skewed emphasis may reflect an historical bias in the taxonomy of the group. For example, "caudal characters" may have traditionally (originally) been used in analyses and subsequent workers have followed the precedent and directed attention to the complex.
2. For some reason a particular region/character complex may be assessed a priori to be of no significance in the evolution of the group, and thus attention has been centered upon the region. This emphasis reflects what Mayr (1969) has termed the "Darwin Principle" in systematics and stresses the use of conservative, "non-functional/non-adaptive" characters in systematic analyses.
3. For some reason a particular region/character complex may be assessed a priori to be of particular significance in the evolution of the group, and thus attention has centered upon the region. This is the opposite position to the preceding case, and emphasizes the use of malleable "functional/adaptive" characters. Although few authors are explicit in their formulation of this approach it is implicit in the works of a number of functional morphologists (e.g., Dullemeijer, 1974; Gutmann, 1977) and "evolutionary" taxonomists (e.g., Szalay, 1981; see also discussion in Cracraft, 1981a).

Each of the above can loosely be viewed as resulting in some sort of taxonomically introduced bias, and subsequent investigation of other morphological complexes would render a range of additional characters for analysis and

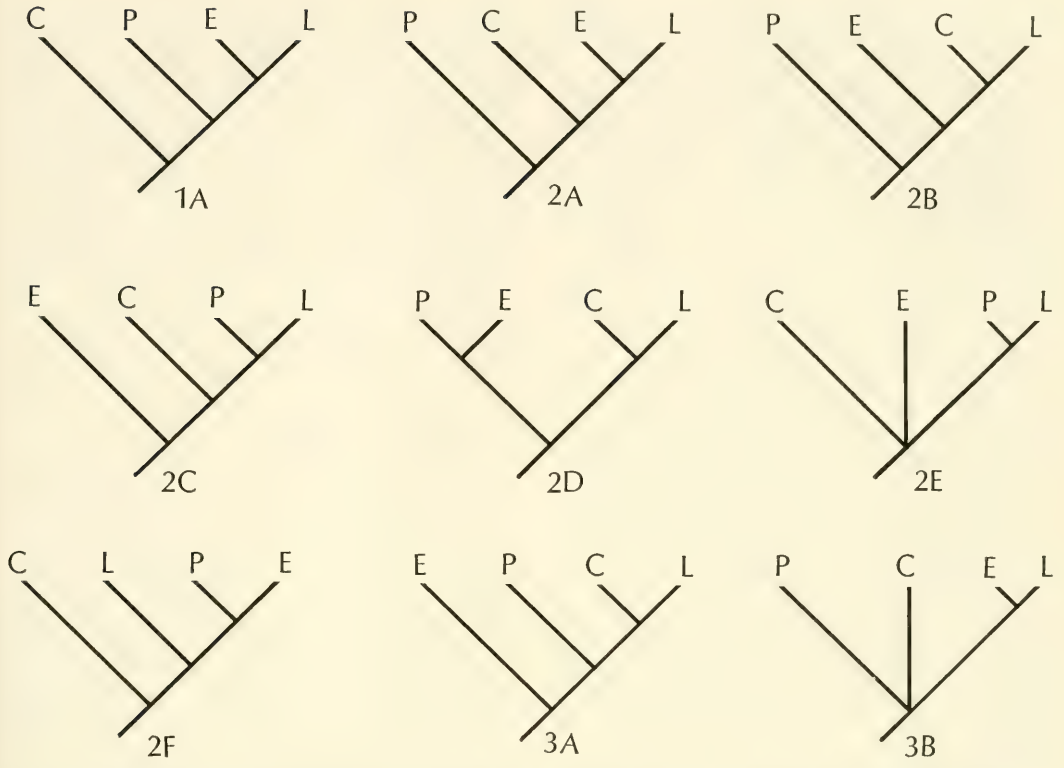

Figure 20. Range of additional trees (of length 27 or less) derivable from the character data entered into the analysis. 1A (length 24), 2A–F (length 26), and 3A–B (length 27). C = Cichlidae, P = Pomacentridae, E = Embiotocidae and L = Labridae.

the predominance of the original complex may be expected to be reduced. This isn't, of course, to say that those original features suddenly become unimportant or insignificant, but only that they no longer predominate.

In view of our conscious effort to locate features other than pharyngeal ones uniting the Labroidei and our inability to find any, we suggest that it is improbable that investigator bias is responsible for the importance of the pharynx in diagnosing the clade. Of course we cannot rule out the possibility that other morphological information does exist and that we have simply not found it yet, but our hypothesis is that such data do not exist.

4. Predominance of the region may simply be a reflection of structural (and/or functional) complexity. As Lauder (1981) quite correctly pointed out, few morphologists have explicitly considered the influence of complexity upon patterns of morphological change. Intuitively at least, it seems that complex systems have a higher likelihood of change than simple ones. If complexity is defined as the number of parameters needed to describe form (Lauder, 1981; Vermeij, 1973), then an increase of complexity will automatically increase the number of possibilities for change in the component elements and in their relations to one another. Complex systems have more potentially stable intermediate states and have, therefore, options for change in design at each level (Lauder, 1981; Simon, 1962).

The euteleostean pharynx is a highly complex construction, composed of many elements and numerous struc-

tural and functional networks of interconnection. Lauder (1983) showed that there is a degree of decoupling between patterns of functional activity and the sequence of structural modification in the euteleostean pharynx. In this complex system overall functioning can be maintained in the face of sequential structural modification. In view of the complexity of the system, and concomitant structural variation, it is perhaps not surprising that so much attention has been centered upon pharyngeal characters in the systematics of euteleostean clades (e.g., Nelson, 1969; Rosen, 1973; Rosen and Parenti, 1981).

We doubt whether a case can be made that the labroid pharynx is more complex than that of other clades; complexity alone does not seem to account for our observation of pharyngeal dominance in labroid systematics.

5. The predominance of any particular region/character complex may indicate that it actually represents some significant and independent locus of evolutionary change.

With all of the caution that the preceding list engenders, we would nonetheless like to speculate that our findings may indicate that the PJA does indeed represent precisely this sort of major locus of evolutionary change for the labroid clade. That features of the pharynx alone seem to characterize the Labroidei indicates that, relative to other systems, this complex underwent extensive restructuring early in the history of the clade. Perhaps, as suggested by Liem (1973), a single change in one aspect of this complex precipitated a major restructuring in other elements of the pharyngeal network. Initial restructuring of the pharynx, a complex considered to be profoundly important in the evolution of the Labroidei (see discussion of the concept of key innovation below), may then have been a very rapid, yet integrated, event.

If this is the case, the pharynx may easily be overemphasized as a source of *systematic* information since many of the characters treated as independent (and equivalent) are a necessary result of the single initial change. The remarkable mirroring of a whole suite of morphological features of the PJA in the phylogenetically disparate labroids and beloniforms would appear to support this inference. Recognition of what constitutes a "unit-character" in a situation such as this is obviously fraught with difficulty.

Key Innovations and the Explanation of Differential Diversity

According to recent studies, features of the pharynx may have had important consequences for the morphologic and taxic diversity of the Labroidei (e.g., Lauder, 1983; Liem, 1973, 1980; Liem and Osse, 1975; Liem and Sanderson, 1986). Early suggestions that the acquisition of a novel structure (e.g., an LPJ suspended by a muscle sling) could profoundly influence the subsequent evolution of a lineage usually involved the idea of the novel feature allowing entry into a new adaptive zone (e.g., Mayr, 1963; Simpson, 1944, 1953, 1959).

Subsequent radiation in an arena of reduced competition gave rise to diverse and/or speciose lineages, the success of which could then be attributed to the acquisition of the unique feature characterizing them. The importance of such an "adaptive breakthrough" in transpecific evolution and the origin of higher taxa has been repeatedly stressed in subsequent explanations of organismic diversity (and enhanced speciation?) (e.g., Jaanusson, 1981; Liem, 1973, 1980; Miller, 1949; Stanley, 1968). A plethora of names for this "distinctive sort of adaptation" (Simpson, 1953) is available (e.g., key adjustments, key inventions, key evolutionary novelties, major adaptive innovations). For ease of discussion we will follow Lauder (1981) in adopting the term key innovation (KI).

Most recently, in a pair of perceptive

and insightful publications Lauder (1981, 1982a) critically analyzed the key innovation concept. His primary criticism, with which we concur, is that a hypothesis that a structure plays a "key" (causal?) role in the subsequent evolution of a lineage is untestable within the framework usually proposed. If an evolutionary novelty is indeed unique, how can any hypothesis regarding its importance be tested by comparison with its influence in independent circumstances? Unique events do not allow a critical analysis of their consequences.

As a solution to this dilemma, Lauder (1981, 1982a) suggested that general attributes (emergent organizational properties) of unique features be sought, so that the consequences of these general features can be compared in both closely related and distantly related taxa. In this sense, it is not only the particular physical features located in compared taxa that are the putative KIs but also the general or emergent properties resulting from them. Lauder provided us with a method to bypass the evolutionary "uniqueness" of specific morphologies by concentrating attention on general, and thus comparable, properties. As an example of such a general property, Lauder (1981) discussed the decoupling of primitively constrained systems and its possible consequences on the subsequent evolution of a taxon. Precisely such a functional decoupling between buccal and pharyngeal jaws, following key innovational pharyngeal specialization, is proposed to have played a central role in the extensive trophic diversification of cichlid fishes (Liem, 1973; Liem and Osse, 1975). The development of a highly integrated PJA (later found to characterize the Labroidei as a whole, see pages 273–288), and the subsequent freeing of the buccal jaws from a major role in food preparation prior to deglutition (Liem's second major function), is held to have resulted in an extreme specialization of the buccal apparatus.". . .The release of the restricting influence of the second major function resulted in the emergence of numerous specializations of collecting mechanisms dealing with dramatically diverse foods." (Liem, 1973: 41). The resultant ability of the clade to exploit a great variety of trophic resources is considered to be of central importance in cichlid trophic diversification, ecological predominance, and explosive speciation (e.g., Fryer and Iles, 1972; Greenwood, 1974, 1984; Liem, 1973, 1980). If this particular PJA configuration was indeed an unique evolutionary novelty then no comparison of its effects in other clades would be possible and its consequences could not be assessed (but see discussion of the beloniform parallel on pages 310–312). However, as decoupling is a general or emergent property transcending the features of any particular system, one can legitimately look elsewhere for clades that exhibit comparable structural and/or functional decoupling. A relationship between decoupling and, for example, morphological diversity between terminal taxa of both clades can now be sought. Following Lauder (1981, 1982a; Liem and Wake, 1985), one may pose the relational hypothesis that the emergence of a general property (Z in Fig. 21A) has consequences for the diversity of terminal taxa (A–D in Fig. 21A). The proposed method of testing this hypothesis is the repeated assessment of diversity (or whatever parameter is being judged) within and between unrelated lineages also possessing this general property (Z′ and Z″, Fig. 21A). If no relationship between the presence of this property and a particular pattern is found, the hypothesis is rejected.

However, if such a comparative test is to be meaningful, one cannot directly compare attributes of the taxa in which the putative KIs occur. Diversity (like species richness) is a relative term and if a clade or set of clades is to be considered diverse (or speciose), this determination can only be made with respect to some meaningful standard of comparison. A consideration of the phylogenetic context of each taxon provides the only meaning-

ful standard for comparison. As is implicit in Hennig (1966: 225) and Lauder (1981, 1982a), it is the sistergroup of the taxon possessing the putative KI that provides the standard by which diversity (or species richness) may be judged (see also excellent discussion in Cracraft, 1981b, 1982).

We would like to emphasize the need for comparison between the clade possessing the putative KI and its sistergroup lacking it (A–D/X in Fig. 21B) in assessments of diversity or species richness. Accordingly comparisons of species number (or diversity) are made between clades that have equivalent histories up to the time of their divergence. They are of equal age, began with equivalent developmental programs, and differ only in those features arising (or re-emerging) after their divergence. In these important features then, the sistergroup is the closest approximation we have to what the lineage under consideration would be like had it not developed the KI (and other evolutionary novelties characterizing it). As illustrated by Figure 21B, testing of hypotheses regarding the role of a key innovation becomes a two step process. Step one (Fig. 21B) provides a measure of the relative diversity of the taxon possessing the putative KI (A–D in Fig. 21B) and its sister group (X in Fig. 21B). In the second step (step 2 in Fig. 21B) relative diversities are then compared *between* independent lineages in which comparable key innovations have arisen (Step 2 in Fig. 21B: E–H to X′ versus I–L to X″). In this way possibly confounding historical factors are held to a minimum and the relative nature of the term diversity (or species richness) is acknowledged and, as far as is possible, is accounted for (but see discussion on pages 312–313).

In past considerations of the key innovation concept it is frequently unclear what exactly the concept is meant to explain. A key innovation is frequently invoked to account for the success of a lineage, but many properties might be used to characterize a particular lineage as successful. For example, enhanced speciation rates, reduced extinction rates, or morphological diversification are all perfectly reasonable criteria of particular kinds of success. In discussions or hypotheses of a key innovation, species richness and morphological diversity are often used interchangeably or treated as if they are so closely related as to render distinction unnecessary. While it may frequently be the case that morphological differentiation is the by-product of the speciation process, it is by no means necessarily so, as is evidenced by the well-documented phenomenon of sibling species (Mayr, 1976; McKaye *et al.*, 1982). Nor is it necessarily the case that morphological diversity within a lineage can be explained simply as the sum of differentiations accompanying speciation (Simpson, 1944, 1953). Even if morphological diversity is the proposed outcome of the origin of a key innovation, it must also be clearly specified what types of features are in fact diversifying. Is it the specific morphological complex involving the key innovation or the organism as a whole that is supposed to undergo change? Any test of the effect of structural features or their emergent properties on the evolution of a lineage will require an explicit prediction of the nature of the consequences of their presence.

The need to precisely specify the nature of the predicted consequences of a key innovation is clearly evident when we consider the development of a pharyngeal muscle sling and Liem's (1973) hypothesis of its effect on subsequent evolution. As described on pages 274–266, within the Beloniformes, one finds a striking morphological parallel between the configu-

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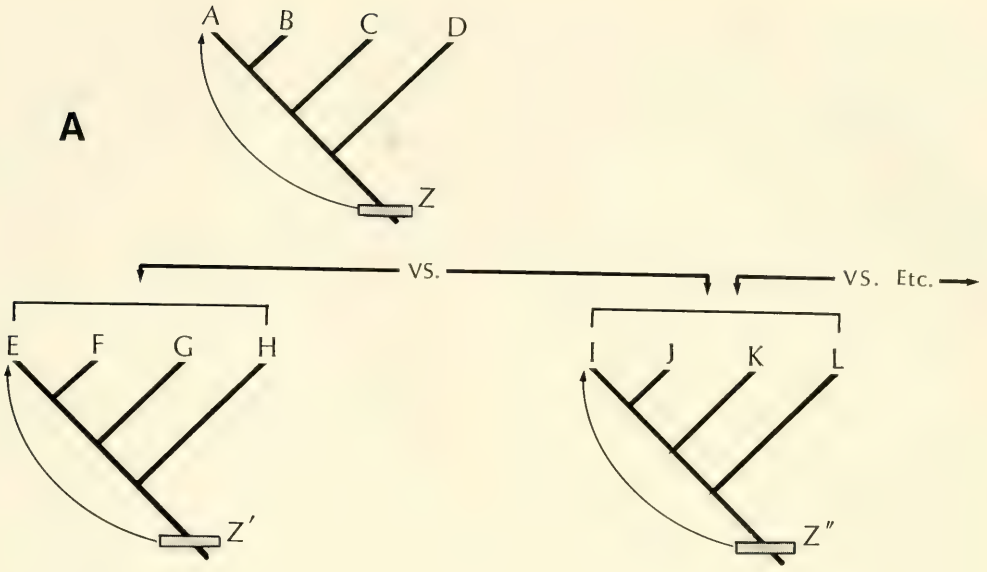
Figure 21. Testing of relational hypotheses involving correlations between the possession of emergent features (Z) and the resultant properties of groups. A. After Lauder (1981); B. Test incorporating initial intracladal sistergroup (X) comparison (step 1) prior to intercladal comparison (step 2). (see page 310 for further explanation of figure).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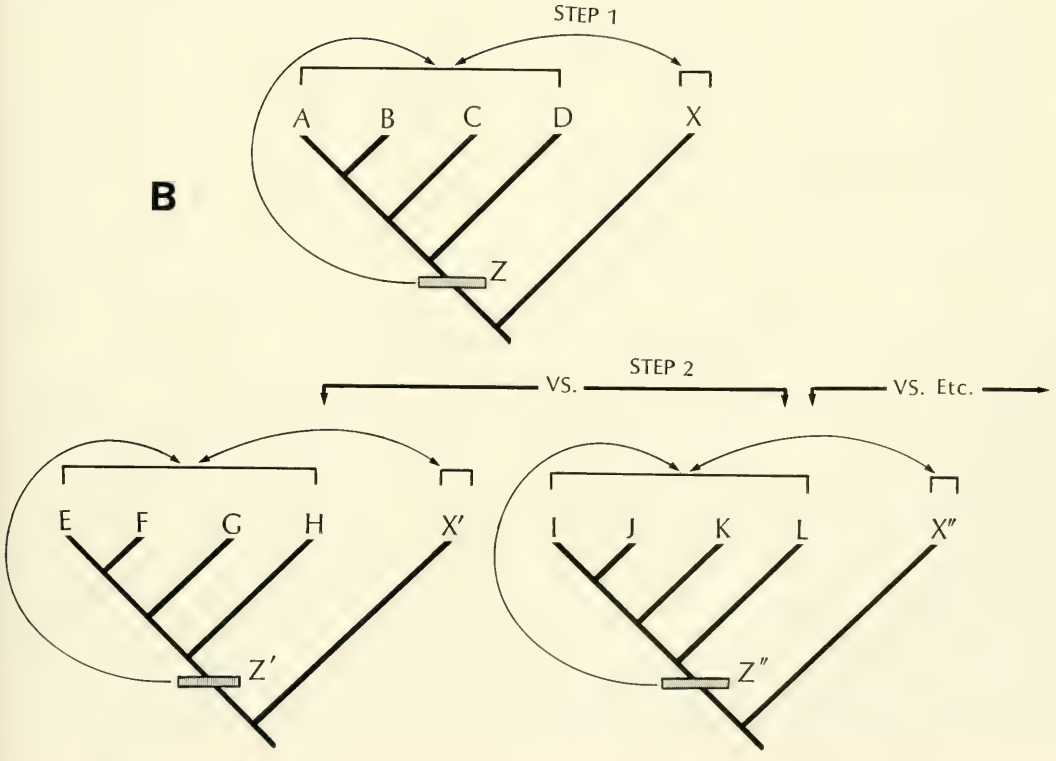
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ration of the PJA of labroids (Fig. 6) and that of the Exocoetoidea (Fig. 2). In these fishes (the Hemiramphidae and Exocoetidae) the fourth levator externus muscle (and a portion of the levator posterior) form a muscle sling supporting the fused fifth ceratobranchial elements. In addition, the dorsal musculature (particularly the transversus dorsalis posterior) is reduced and the articulatory facets of the third pharyngobranchials are exposed to form a diarthrosis with a well-developed neurocranial apophysis (Fig. 2E). The Scomberescoidea lack these features although, like the Exocoetoidea, they possess a completely united LPJ in which no trace of a median suture is evident. The LPJ also bears a well-developed median keel onto which the transversus ventralis muscle inserts.

The fortuitous morphological mirroring of aspects of the labroid PJA by that of non-adrianichthyoid beloniforms allows at least one test of the evolutionary consequences of a putative key innovation in these phylogenetically disparate assemblages. However, for this test to be unambiguous we need a clearly stated hypothesis of the consequences of the key innovation. For example, if our prediction is increased species number, we find that the Exocoetoidea is indeed more successful than its sister lineage, the Scomberesocoidea (Fig. 7; 135+ species in the Exocoetoidea versus 36 species in the Scomberesocoidea, Nelson, 1984). This would seem to support the hypothesis of this particular pharyngeal configuration being key to the taxic success of a lineage. Likewise, if diversity of the trophic apparatus as a whole is the predicted outcome, then the wide range of tooth morphologies of both the PJA and the buccal jaws found in the Exocoetoidea relative to the Scomberesocoidea (Collette, 1966, 1974, 1976; Parin, 1961) would lend support to this hypothesis. However, the Scomberesocoidea exhibits a far greater diversity of LPJ form (but not dentition) than does its sister lineage (e.g., compare figs. 2, 3 of Collette, 1966 with fig. 16 of Parin, 1961). In this respect, the Exocoetoidea can be considered to lack significant diversity, indicating that the development of a muscle sling has not resulted in an overall pharyngeal diversification. Thus it would seem that clarification and explicit statement of the proposed consequences of the development of the key innovation are a necessary prerequisite for the generation of hypotheses about generality of effects and the role of KIs in evolution.

Despite the methodological refinement of Lauder's scheme outlined here (Fig. 21B), rigorous testing of historical hypotheses still presents difficulties. Even given a reasonable number of independent clades in which to conduct comparisons, it seems unlikely that comparisons of lineages sharing a putative KI with their respective sistergroups (the first step in our analysis) will always lead to unambiguous statements regarding the role of those innovations in, for example, cladogenesis. If our hypothesis is that the presence of a key innovation is somehow implicated in enhanced speciation rates (or morphological diversification), this would be refuted by finding a clade with a comparable key innovation which is depauperate relative to its sistergroup. However, the question immediately arises as to how comparable these sister lineages are with respect to the suite of extrinsic factors acting upon them after their origin (see also Cracraft, 1982). Any differences in species richness or morphological diversity found in the two clades might as easily be the result of differences in their habitat (e.g., estuary versus coral reef), vicariant history (e.g., mid-ocean versus shallow lake basin), later behavioral developments, and so on. Almost inevitably there will be many ways in which the factors affecting species richness or diversity will differ due to the independent histories of sister lineages subsequent to their phylogenetic origin.

Likewise, the second phase of the analysis (i.e., comparison of independent clades

within which the key innovation arises; step 2 in Fig. 21B) presents its own difficulties. It might not be the case that the same evolutionary "novelty" or property will have equivalent effects when arising in different phylogenetic contexts. How likely is it that two different lineages, each with its own intrinsic morphological constraints, developmental pattern, etc. will respond in the same way to the appearance of the "same" evolutionary novelty or property? While each appearance of the evolutionary novelty would indeed be independent, it might not be comparable because the innovation would, in each case, appear against a unique historical background, a set of existing functional constraints, and would be subject in the course of subsequent evolution to a unique set of extrinsic factors. The consequences of, for example, decoupling in one component of the trophic apparatus (e.g., the buccal jaws) may be very different, depending on the limitations imposed by primitive constraints on other components of the trophic apparatus (e.g., pharyngeal jaws). While the first step of the analysis would not be affected, since the network of constraints would be primitive for both taxa (A–D *and* X; Fig. 21B), the nature of the constraints affecting independent taxa (E–H to X′ vs. I–L to X″; Fig. 21B) might differ greatly and thus have different interactions with the putative key innovation. Even if an innovation may be implicated in cladogenesis (e.g., Stanley, 1975) or diversification in one case, in another case it might arise in a context in which pre-existing functional networks or subsequent environmental influences are so constraining as to overwhelm its role in diversification or cladogenesis. Thus, assertions about the influence of key innovations, even when situated in a strictly phylogenetic framework, run the risk of being reduced to particularistic explanations about unique events in an unique historical arena.

Despite the problems alluded to above, we concur with Lauder (1982b: 66) that "The key to discovering the limits to deterministic explanation in the historical record will be the extent to which general historical pathways in the transformation of biological design are revealed by a phylogenetic analysis of structural and functional patterns." The structural approach to historical patterns advocated by Lauder renders phylogeneticists with a method with which to begin that search. Discovery of such general historical pathways will have profound implications regarding the nature of the evolutionary process.

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LITERATURE CITED

AERTS, P. 1982. Development of the musculus levator externus IV and the musculus obliquus posterior in *Haplochromis elegans* Trewavas, 1933 (Teleostei: Cichlidae): A discussion on the shift hypothesis. Journal of Morphology, **173:** 225–235.

ANKER, G. CH. 1978. The morphology of the head muscles of a generalized *Haplochromis* species: *H. elegans* Trewavas, 1933 (Pisces, Cichlidae). Netherlands Journal of Zoology, **28:** 234–271.

BARLOW, G. W., AND J. W. MUNSEY. 1976. The Red Devil-Midas-Arrow cichlid species complex in Nicaragua, pp. 359–369. *In* T. B. Thorson (ed.), Investigations of the Ichthyofauna of Nicaraguan Lakes. Lincoln, Nebraska: School of Life Sciences, University of Nebraska. x + 663 pp.

BAREL, C. D. N., F. WITTE, AND M. J. P. VAN OIJEN. 1976. The shape of the skeletal elements in the head of a generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae). Netherlands Journal of Zoology, **26:** 163–265.

BERG, L. S. 1940. Classification of fishes and fish-like vertebrates, living and fossil. Russian and English lithoprint, **1947:** 87–517. Ann Arbor, Michigan.

BERTIN, L., AND C. ARAMBOURG. 1958. Superordre des Teleosteens, pp. 2204–2500. *In* P. Grasse (ed.), Traite de Zoologie, Anatomie, Systematique, Biologie. Volume 13 Agnathes et Poissons. Paris: Grassé.

BRETT, J. R. 1979. Some morphological and behavioural adaptations of the pile perch (*Rhacochilus vacca*) feeding on mussels (*Mytilus edulis*). Canadian Journal of Zoology, **57:** 658–664.

CLAEYS, H., AND P. AERTS. 1984. Note on the compound lower pharyngeal jaw operators in *Astatotilapia elegans* (Trewavas), 1933 (Teleostei: Cichlidae). Netherlands Journal of Zoology, **34:** 210–214.

COLLETTE, B. B. 1966. *Belonion*, a new genus of fresh-water needlefishes from South America. American Museum Novitates, **2274:** 1–22.

———. 1974. South American freshwater needlefishes (Belonidae) of the genus *Pseudotylosaurus*. Zoologische Mededelingen. Leiden, **48**(16): 169–186.

———. 1976. Indo-West Pacific halfbeaks (Hemiramphidae) of the genus *Rhynchorhamphus* with descriptions of two new species. Bulletin of Marine Science, **26**(1): 72–98.

COLLETTE, B. B., G. E. GOWEN, N. V. PARIN, AND S. MITO. 1984. Beloniformes: Development and relationships, pp. 335–354. *In* H. G. Moser (ed.-in-chief), Ontogeny and Systematics of Fishes. Special Publications of the American Society of Ichthyologists and Herpetologists No. 1. Lawrence, KS: Allen Press. 760 pp.

CRACRAFT, J. 1981a. The use of functional and adaptive criteria in phylogenetic systematics. American Zoologist, **21:** 21–36.

———. 1981b. Pattern and process in paleobiology: the role of cladistic analysis in systematic paleontology. Paleobiology, **7**(4): 456–468.

———. 1982. A non-equilibrium theory for the rate control of speciation and extinction and the origin of macroevolutionary patterns. Systematic Zoology, **31**(4): 348–365.

DE MARTINI, E. E. 1969. A correlative study of the ecology and comparative feeding mechanism morphology of the Embiotocidae (surf-fishes), as evidence of the family's adaptive radiation into available ecological niches. The Wasmann Journal of Biology, **27**(2): 117–247.

DIETZ, P. A. 1921. Beitrage zur Kenntnis der Keifer- und Kiemengogenmuskelatur der Teleosteir. Mitteilungen aus der Zoologischen Station zu Neapel. Berlin, **22**(13–16): 433–457.

DINGERKUS, G., AND L. D. UHLER. 1977. Enzyme clearing of Alcian Blue stained whole small vertebrates for demonstration of cartilage. Stain Technology, **52**(4): 229–232.

DULLEMEIJER, P. 1974. Concepts and Approaches in Animal Morphology. Assen, The Netherlands: Van Gorcum. xii + 270 pp.

———. 1980. Functional morphology and evolutionary biology. Acta Biotheoretica, **28:** 151–250.

DULLEMEIJER, P., AND C. D. N. BAREL. 1977. Functional morphology and evolution. *In* M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), Major Patterns in Vertebrate Evolution. London: Plenum Press. ix + 908 pp.

ELDREDGE, N., AND J. CRACRAFT. 1980. Phylogenetic Patterns and the Evolutionary Process. Methods and Theory in Comparative Biology. New York: Columbia University Press. 349 pp.

EMERY, A. R. 1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. Bulletin of Marine Science, **23**(3): 649–770.

FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. American Naturalist, **106:** 645–668.

FORD, E. 1937. Vertebral variation in teleostean fishes. Journal of the Marine Biological Society of the United Kingdom. Plymouth, **22:** 1–37. Figs. 1–18, Pls. 1–16.

FRYER, G., AND T. D. ILES. 1972. The Cichlid Fishes of the Great Lakes of Africa. Their Biology

and Evolution. Edinburgh: Oliver and Boyd. 641 pp.

FUTUYMA, D. J. 1979. Evolutionary Biology. Greenfield, Mass.: Sinauer Associates, Inc. x + 565 pp.

GOBALET, K. W. 1980. Functional morphology of the head of parrotfishes of the genus *Scarus*. Ph.D. thesis, University of California at Davis.

GOEDEL, W. VON 1974a. Beitrage zur vergleichenden und funktionellen Anatomie des Kopfes von *Tilapia* (Cichlidae, Teleostei). Teil. 1 Zoologische Jahrbuecher Anatomie, **92:** 220–274.

———. 1974b. Beitrage zur vergleichenden und funktionellen Anatomie des Kopfes von *Tilapia* (Cichlidae, Teleostei). Teil. 2 Zoologische Jahrbuecher Anatomie, **92:** 321–383.

GOMON, M. F., AND J. P. PAXTON. 1986. A revision of the Odacidae, a temperate Australian-New Zealand labrid family. Indo-Pacific Fishes, **8:** 1–57.

GOSLINE, W. A. 1961. The perciform caudal skeleton. Copeia, **1961**(3): 265–270.

———. 1966. The limits of the fish family Serranidae, with notes on other lower percoids. Proceedings of the California Academy of Sciences, **33**(6): 91–112.

GREENWOOD, P. H. 1974. Cichlid fishes of Lake Victoria, east Africa: the biology and evolution of a species flock. Bulletin of the British Museum of Natural History (Zoology) supplement, **6:** 1–134.

———. 1978. A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes. Bulletin of the British Museum of Natural History (Zoology), **33:** 297–323.

———. 1984. African cichlids and evolutionary theories, pp. 141–154. *In* A. A. Echelle and I. Kornfield (eds.), Evolution of Fish Species Flocks. Orono, Maine: University of Maine at Orono Press. 257 pp.

———. 1985. Notes on the anatomy and phyletic relationships of *Hemichromis* Peters, 1858. Bulletin of the British Museum of Natural History (Zoology), **48:** 131–171.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History, **131:** 339–455.

GUNTHER, A. 1880. An Introduction to the Study of Fishes. Edinburgh: Adam and Charles Black. xvi + 720 pp.

GUTMANN, W. F. 1977. Phylogenetic reconstruction: theory, methodology, and application to chordate evolution, pp. 645–669. *In* M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), Major Patterns in Vertebrate Evolution. London: Plenum Press. ix + 908 pp.

HENNIG, W. 1966. Phylogenetic Systematics. Urbana: University of Illinois Press. 263 pp.

HIXON, M. A. 1980. Competitive interactions between California reef fishes of the genus *Embiotoca*. Ecology, **61**(4): 918–931.

HOLLISTER, G. 1936. Caudal skeleton of Bermuda shallow water fishes. I. Order Isospondyli: Elopidae, Megalopidae, Albulidae, Clupeidae, Dussumieriidae, Engraulidae. Zoologica, **21:** 257–290.

———. 1937. Caudal skeleton of Bermuda shallow water fishes. II. Order Percomorphi, Suborder Percesoces: Atherinidae, Mugilidae, Sphyreanidae. Zoologica, **22:** 265–279.

JAANUSSON, V. 1981. Functional thresholds in evolutionary progress. Lethaia, **14:** 251–260.

JOHNSON, G. D. 1980. The limits and relationships of the Lutjanidae and associated families. Bulletin Scripps Institution of Oceanography, **24:** 1–114.

———. 1984. Percoidei: Development and relationships, pp. 464–498. *In* H. G. Moser (ed.-in-chief), Ontogeny and Systematics of Fishes. Special Publications of the American Society of Ichthyologists and Herpetologists No. 1. Lawrence, KS: Allen Press. 760 pp.

JORDAN, D. S. 1905. Guide to the Study of Fishes. Volume II. New York: Henry Holt and Co. xxii + 599 pp.

KAUFMAN, L., AND K. F. LIEM. 1982. Fishes of the suborder Labroidei (Pisces: Perciformes): Phylogeny, ecology, and evolutionary significance. Breviora. Museum of Comparative Zoology, Harvard University, **472:** 1–19.

LAUDER, G. V. 1981. Form and function: structural analysis in evolutionary morphology. Paleobiology, **7**(4): 430–442.

———. 1982a. Historical biology and the problem of design. Journal of Theoretical Biology, **97:** 57–67.

———. 1982b. Introduction, pp. xi–xlv. *In* E. S. Russell, Form and Function. A Contribution to the History of Animal Morphology. Chicago: University of Chicago Press. xlv + 383 pp.

———. 1983. Functional design and evolution of the pharyngeal jaw apparatus in euteleostean fishes. Zoological Journal of the Linnean Society of London, **77:** 1–38.

LAUDER, G. V., AND K. F. LIEM. 1983. The evolution and interrelationships of the actinopterygian fishes. Bulletin of the Museum of Comparative Zoology, Harvard University, **150:** 95–197.

LAUR, D. R., AND A. E. EBELING. 1983. Predator-prey relationships in surfperches. Environmental Biology of Fishes, **8:** 217–229.

LIEM, K. F. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Systematic Zoology, **22:** 425–441.

———. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. American Zoologist, **20:** 295–314.

———. 1986. The pharyngeal jaw apparatus of the Embiotocidae (Teleostei): A functional and evolutionary perspective. Copeia, **1986**(2): 311–323.

LIEM, K. F., AND J. W. M. OSSE. 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. American Zoologist, **15:** 427–454.

LIEM, K. F., AND P. H. GREENWOOD. 1981. A functional approach to the phylogeny of the pharyngognath teleosts. American Zoologist, **21:** 83–101.

LIEM, K. F., AND D. B. WAKE. 1985. Morphology: Current approaches and concepts, pp. 366–377. *In* M. Hildebrand, D. Bramble, K. F. Liem, and D. B. Wake (eds.), Functional Vertebrate Morphology. Cambridge, Mass.: The Belknap Press of Harvard University Press. 430 pp.

LIEM, K. F., AND L. SANDERSON. 1986. The pharyngeal jaw apparatus of labrid fishes: a functional morphological perspective. Journal of Morphology, **187:** 143–158.

MADDISON, W. P. 1986. MacClade version 1. Program and user's manual. Privately distributed.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Systematic Zoology, **33:** 83–103.

MAYR, E. 1963. Animal Species and Evolution. Cambridge, Mass.: Belknap Press of Harvard University Press. xiv + 797 pp.

———. 1969. Principles of Systematic Zoology. New York: Columbia University Press. xxxvii + 334 pp.

———. 1976. Sibling or cryptic species, pp. 510–514. *In* E. Mayr (ed.), Evolution and the Diversity of Life. Selected Essays. Belknap Press of Harvard University Press. ix + 721 pp.

MCKAYE, K. R., T. KOCHER, P. REINTHAL, AND I. KORNFIELD. 1982. A sympatric sibling species complex of *Petrotilapia* Trewavas from Lake Malawi analysed by enzyme electrophoresis (Pisces, Cichlidae). Zoological Journal of the Linnean Society of London, **76:** 91–96.

MILLER, A. H. 1949. Some ecologic and morphologic considerations in the evolution of higher taxonomic categories, pp. 84–88. *In* E. Mayr and E. Schuz (eds.), Ornithologie als Biologische Wissenschaft. Heidelberg: Carl Winter.

MORRIS, S. L. 1982. The osteology and relationships of the Embiotocidae (Pisces). Ph.D. thesis. Oregon State University.

MORRIS, S. L., AND A. J. GAUDIN. 1982. Osteocranial development of the viviparous surfperch *Amphistichus argenteus* (Pisces: Embiotocidae). Journal of Morphology, **174:** 95–120.

MÜLLER, J. 1843. Nachtrage zu der Abhandlung uber die naturlich Familien der Fische. Archive für Naturgeschichte, **9:** 381–384.

NELSON, G. J. 1967a. Gill arches of some teleostean fishes of the families Girellidae, Pomacentridae, Embiotocidae, Labridae and Scaridae. Journal of Natural History, **1:** 289–293.

———. 1967b. Branchial muscles in some generalized teleostean fishes. Acta Zoologica, Stockholm, **48:** 277–288.

———. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bulletin of the American Museum of Natural History, **141**(4): 480–552.

NELSON, G. J., AND N. I. PLATNICK. 1981. Systematics and Biogeography. Cladistics and Vicariance. New York: Columbia University Press. xi + 567 pp.

NELSON, J. S. 1984. Fishes of the World. Toronto: John Wiley and Sons. xv + 523 pp.

NORMAN, J. R. 1966. A Draft Synopsis of the Orders, Families and Genera of Recent Fishes and Fish-Like Vertebrates. 4. Trustees of the British Museum (Natural History). 649 pp.

PARENTI, L. R. 1984. A taxonomic revision of the andean killifish genus Orestias (Cyprinodontiformes, Cyprinodontidae). Bulletin of the American Museum of Natural History, **178**(2): 107–214.

PARIN, N. V. 1961. The bases for the classification of the flying-fishes (families Oxyporhamphidae and Exocoetidae). Trudy Instituta Okeanologii, Akademiya Nauk SSSR, Moskva, **43:** 92–183. Translation No. 67 Systematics Lab., NMFS, Washington.

PATTERSON, C. 1968. The caudal skeleton of Mesozoic acanthopterygian fishes. Bulletin of the British Museum of Natural History (Geology), **17**(2): 47–102.

———. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton, pp. 77–121. *In* S. M. Andrews, R. S. Miles, and A. D. Walker (eds.), Problems in Vertebrate Evolution. London: Academic Press. 411 pp.

PELLEGRIN, J. 1903. Contribution a l'étude anatomique, biologique et taxonomique des poissons de la famille des cichlidés. Mémoires Société Zoologique de France, **16:** 41–402.

REGAN, C. T. 1913. The classification of percoid fishes. Annals and Magazine of Natural History, (8)**12:** 111–145.

ROGNES, K. 1973. Head skeleton and jaw mechanism in the Labrinae (Teleostei: Labridae) from Norwegian waters. Acta Universitatis Bergensis, Series Mathematica Rerumque Naturalium, **4:** 1–149.

ROSEN, D. E. 1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. Bulletin of the American Museum of Natural History, **127**(5): 219–267.

———. 1973. Interrelationships of higher euteleostean fishes, pp. 397–513. *In* P. H. Greenwood, R. S. Miles, and C. Patterson (eds.), Interrelationships of Fishes. London: Academic Press. 536 pp.

———. 1985. An essay on euteleostean classification. American Museum Novitates, **2827:** 1–45.

ROSEN, D. E., AND P. H. GREENWOOD. 1976. A fourth neotropical species of synbranchid eel and the phylogeny and systematics of synbranchi-

form fishes. Bulletin of the American Museum of Natural History, **157:** 1–70.

ROSEN, D. E., AND L. R. PARENTI. 1981. Relationships of *Oryzias*, and the groups of atherinomorph fishes. American Museum Novitates **2719:** 1–25.

ROSEN, D. E., AND C. PATTERSON. 1969. The structure and relationships of the paracanthopterygian fishes. Bulletin of the American Museum of Natural History, **141**(3): 357–474.

RUSSELL, E. S. 1982. Form and Function. A Contribution to the History of Animal Morphology. Chicago: Chicago University Press. xlv + 383 pp.

SCHMITT, R. J., AND J. A. COYER. 1982. The foraging ecology of sympatric marine fish in the genus *Embiotoca* (Embiotocidae): Importance of foraging behavior in prey size selection. Oecologia, **55:** 369–378.

SIMON, H. A. 1962. The architecture of complexity. Proceedings of the American Philosophical Society, **106:** 467–482.

SIMPSON, G. G. 1944. Tempo and Mode in Evolution. New York: Columbia University Press. xvii + 237 pp.

———. 1953. The Major Features of Evolution. New York: Columbia University Press. xx + 434 pp.

———. 1959. The nature and origin of supraspecific taxa. Cold Spring Harbor Symposia on Quantitative Biology, **24:** 255–271.

SMITH, C. L., AND R. M. BAILEY. 1961. Evolution of the dorsal-fin supports of percoid fishes. Papers of the Michigan Academy of Science, Arts, and Letters, **XLVI:** 345–363.

———. 1962. The subocular shelf of fishes. Journal of Morphology, **110**(1): 1–17.

SPRINGER, V. G. 1968. Osteology and classification of the fishes of the family Bleniidae. Bulletin of the United States National Museum No. 284. 83 pp.

SPRINGER, V. G., AND W. C. FREIHOFER. 1976. Study of the monotypic fish family Pholidichthyidae (Perciformes). Smithsonian Contributions to Zoology, **216:** 1–43.

STANLEY, S. M. 1968. Post-paleozoic adaptive radiation of infaunal bivalve molluscs—a consequence of mantle fusion and siphon formation. Journal of Paleontology, **42**(1): 214–229.

———. 1975. A theory of evolution above the species level. Proceedings of the National Academy of Sciences, **72**(2): 646–650.

———. 1979. Macroevolution. Pattern and Process. San Francisco: W. H. Freeman and Co. xi + 332 pp.

STEVENS, P. F. 1980. Evolutionary polarity of character states. Annual Review of Ecology and Systematics, **11:** 333–358.

STIASSNY, M. L. J. 1980. The anatomy and relationships of two genera of African cichlid fishes. Ph.D. thesis, University of London.

———. 1981. The phyletic status of the family Cichlidae (Pisces, Perciformes): A comparative anatomical investigation. Netherlands Journal of Zoology, **31:** 275–314.

———. 1982. The relationships of the neotropical genus *Cichla* (Perciformes, Cichlidae): a phyletic analysis including some functional considerations. Journal of the Zoological Society of London, **197:** 427–453.

———. 1986. The limits and relationships of the acanthomorph teleosts. Journal of Zoology, London (B), **1:** 411–460.

———. in press. Cichlid intrafamilial relationships and the placement of the Neotropical genus *Cichla* (Perciformes: Labroidei). Journal of Natural History.

STRAUSS, R. 1984. Allometry and functional feeding morphology in haplochromine cichlids, pp. 217–229. *In* A. A. Echelle and I. Kornfield (eds.), Evolution of Fish Species Flocks. Orono: University of Maine at Orono Press. 257 pp.

SZALAY, F. S. 1981. Functional analysis and the practice of the phylogenetic methods as reflected by some mammalian studies. American Zoologist, **21:** 37–45.

SWOFFORD, D. L. 1985. Phylogenetic Analysis Using Parsimony. Version 2.4 User's Manual. Champaign: Illinois Natural History Survey.

TARP, F. H. 1952. A revision of the family Embiotocidae (the surfperches). California Department of Fish and Game Fish Bulletin, No. **88:** 1–99.

TRAVERS, R. A. 1981. The interarcual cartilage: a review of its development, distribution and value as an indicator of phyletic relationships in euteleostean fishes. Journal of Natural History, **15:** 853–871.

———. 1984a. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes. Part I: Anatomical descriptions. Bulletin of the British Museum of Natural History, **46:** 1–133.

———. 1984b. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes. Part II: Phylogenetic analysis. Bulletin of the British Museum of Natural History, **47**(2): 83–150.

TREWAVAS, E. 1973. On the cichlid fishes of the genus *Pelmatochromis* with proposal of a new genus for *P. congicus*; on the relationship between *Pelmatochromis* and *Tilapia* and the recognition of *Sarotherodon* as a distinct genus. Bulletin of the British Museum of Natural History (Zoology), **25**(1): 3–26.

VANDEWALLE, P. 1973. Osteologie caudale des Cichlidae (Pisces: Teleostei). Bulletin Biologique de la France et de la Belgique, **107:** 275–289.

VERMEIJ, G. 1973. Adaptation, versatility, and evolution. Systematic Zoology, **22:** 466–477.

VRBA, E. S. 1980. Evolution, species and fossils: How does life evolve? South African Journal of Science, **76:** 61–84.

WATROUS, L. E., AND Q. D. WHEELER. 1981. The outgroup comparison method of character analysis. Systematic Zoology, **30:** 1–11.

WHITE, M. J. D. 1978. Modes of Speciation. San Francisco: W. H. Freeman and Co. vii + 455 pp.

WILEY, E. O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. New York: John Wiley and Sons. xv + 439 pp.

WINTERBOTTOM, R. 1974. A descriptive synonomy of the striated muscles of the Teleostei. Proceedings of the Academy of Natural Sciences of Philadelphia, **125:** 225–317.

WITTE, F. 1984. Ecological differentiation in Lake Victoria haplochromines: comparison of cichlid species flocks in African lakes, pp. 155–167. *In* A. A. Echelle and I. Kornfield (eds.), Evolution of Fish Species Flocks. Orono: University of Maine at Orono Press. 257 pp.

YAMAOKA, K. 1978. Pharyngeal jaw structure in labrid fish. Publications of the Seto Marine Biological Laboratory, **24**(4/6): 409–426.

———. 1980. Some pharyngeal jaw muscles of *Calotomus japonicus* (Scaridae, Pisces). Publications of the Seto Marine Biological Laboratory, **25**(5/6): 315–322.

APPENDIX 1

Data Matrix Used in Character Analysis

Taxa/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Plesiomorphic	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cichlidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1
Embiotocidae	1	1	1	0	0	0	0	1	1	1	0	0	0	1	1
Labridae	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Pomacentridae	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0

The characters are:

1. LPJ with no trace of a central suture, and with pharyngeal teeth implanted directly over the midline.
2. Urohyal articulates with basibranchial one.
3. Absence of musculus cranio-pharyngobranchialis 2 muscle.
4. LPJ "Y-shaped" with short body and elongate lateral horns.
5. Obliquus ventralis IV and rectus ventralis V insert separately onto the semicircular ligament system.
6. Basibranchial one bears a large keel-like ventral extension.
7. Uroneural fused with the urostyle.
8. Second pharyngobranchial toothplate absent.
9. Fourth upper toothplate either markedly reduced or entirely lacking.
10. Interarcual cartilage absent.
11. Reduced number of caudal epurals.
12. Two or fewer predorsal bones.
13. Endopterygoid shelf absent and adductor arcus palatini inserts onto medial face of the suspensorium.
14. Extrascapular bone fused to the parietal.
15. Hemal arch of the antepenultimate caudal vertebrae fused with the centrum.

APPENDIX 2

Abbreviations Used in Figures

AD5	Adductor 5
ART.Z	Articulation zone
BB1–4	Basibranchial 1–4
BHY	Basihyal
CB1–5	Ceratobranchial 1–5
CL	Cleithrum
CT	Connective tissue
"EHR"	"Epihemal ribs"
EP1–4	Epibranchial 1–4
EPR	Epipleurals
INTARC.C	Interarcual cartilage
HBR	Hypobranchial
L.BB3/UHY	Basibranchial3/urohyal ligament
LE4	Fourth levator externus muscle
LE_4 + OP	Fourth levator externus and obliquus posterior
LP	Levator posterior muscle
LPJ	Lower pharyngeal jaw
LT. HORN	Lateral horn
OBL IV	Obliquus ventralis IV
OP	Obliquus posterior muscle
MC. P2	Cranio-pharyngobranchialis 2
MT. E2	Transverse epibranchialis 2
MT. P2	Transversus pharyngobranchialis 2
NC. AP	Neurocranial apophysis
PB1-3	Pharyngobranchial 1–3
PB3-TP	Pharyngobranchial 3 toothplate
PB2-3-TP	Toothplate of PB 2–3
PB3-FC	Articulation facet of PB3
PHC.E	Pharyngocleithralis externus
PHC.I	Pharyngocleithralis internus
PHY	Pharyngohyoideus
PR	Pleural rib
REC.V	Rectus ventralis V
SEMICIRC.LIG	Semicircular ligament system
tA_1	Tendon of A_1 division of adductor mandibulae
TDP	Transversus dorsalis posterior
TV IV-V	Transversus ventralis IV–V
UHY	Urohyal
UP4	Fourth upper toothplate

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SYSTEMATICS AND LEVELS OF COVARIATION IN *CERION* FROM THE TURKS AND CAICOS ISLANDS

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ABSTRACT. *Cerion*, the most morphologically diverse of all pulmonate genera, has been vastly oversplit in such a way that existing names form an incoherent pattern of variation within and among islands. We have reduced the 300-odd taxa of northern Bahamian *Cerion* to a half-dozen species with consistent and predictable distributions. This study represents our first attempt to apply our ecogeographic and biometric methods to the different *Cerion* fauna of the southeastern Bahamas.

The dozen available names, inconsistently distributed about the islands of the Turks and Caicos banks, reduce to three valid species: *Cerion regina*, present on all islands as Turks and Caicos representative of the "tapering morphotype," the predominant and characteristic *Cerion* of this entire region; *C. lewisi*, a Cuban migrant restricted to islands of the western Caicos Bank; and *C. blandi*, misattributed to the *C. glans* complex in the past, but actually an immigrant population of the *C.* (*Umbonis*) stock, confined to Salt Cay on the Turks Bank and hybridizing with local *C. regina*.

Biometric patterns based on factor analyses of mean vectors for all samples reveal order without exception at a series of descending levels. Clustering of samples can be interpreted as results of meaningful patterns in covariance among measures defining the axes. At the most inclusive level of all samples on all islands, each of three principal axes captures the distinctive morphological features of a taxon. Therefore, axes reflect taxonomic diversity and the contingent histories of migrations. At the next lower level of variation (among samples within *C. regina* on all islands), island groups are distinguished by patterns of covariation that express developmental rules of growth and allometry within a coherent *Cerion* ground plan, not the accidents of history revealed in the higher-level analysis among taxa. A smooth morphometric cline, connecting all islands of the Caicos Bank, unites the two major taxa of previous interpretation into a continuous array, and forms the basis for our decision to synonymize all samples of the tapering morphotype as *C. regina*. At a third level of variation (*C. regina* within our best-sampled island of South Caicos), we detect coherence based upon geometric constraints of growth for any coiled shell. Finally, specimens within samples follow similar patterns of covariance, indicating that general rules of growth apply to the conceptually different styles of within- and among-sample variation.

I. The Problem and Promise of *Cerion*

Copious variation in genetically-resolvable patterns of shell coloration has secured for several pulmonate genera the status of evolutionary "classics" (Cain and Currey, 1963 on *Cepaea*; Crampton, 1916, 1925, 1932 and Murray and Clarke, 1980 on *Partula*; Gulick, 1905 and later studies on Hawaiian *Achatinella*, for example). Yet, although remarkable variation in morphology also distinguishes several pulmonate genera from most other mollusks, this source of insight has not been well exploited by evolutionary biologists—in part because the classic genera for studies of color are not particularly variable in form.

Cerion, a widespread West Indian land snail favoring coastal, carbonate substrates, may be the most morphologically diverse of all pulmonate genera, with variation in shell height from 5 to 70 mm, and in shape from pencils to golf balls. We understand the formal basis for this geometric diversity (Gould, 1984b; Gould and Woodruff, 1986; Woodruff and Gould, 1980), but little of its genetic and developmental foundation. The potential for such unparalleled diversity arises from two aspects of growth: first, the complex, ba-

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sically tripartite allometry of all *Cerion* ontogenies (a juvenile button or triangle, followed by an adult "barrel" with little increase in width accompanying major growth in height, and a final change in coiling before secretion of the definitive adult lip); second, the ordering of growth patterns into several interacting but mutually dissociable covariance sets of coordinated characters. This complex allometry provides great scope for translating small heterochronic effects into major changes in adult form, while the potential independence of covariance sets enjoins both forced correlations within sets (further translating small inputs into complex outputs) and substantial play for novel combinations (by independent change between sets). *Cerion*, in short, is a premier subject for students of form.

Yet *Cerion*'s promise has been impeded by two related "myths" propagated by its traditional literature (particularly Maynard, 1889; Maynard and Clapp, 1919–26). First, *Cerion*'s extreme lability in form has inspired the construction of a bloated taxonomy of some 600 taxa, about half from the Bahamas where we have concentrated our studies (see Clench, 1957). Nearly all named taxa of *Cerion* hybridize freely, and few genuine biological species exist. The second *Cerion* myth holds that the geographic distribution of these formally designated taxa forms a basically incoherent spread, implicating capricious and distant transport by hurricanes as the primary mode of colonization. Admittedly, the placement of existing names on maps implies chaos of this sort, but the traditional taxonomy is fundamentally erroneous (Gould and Woodruff, 1978, 1986, for example).

We have been studying the systematics and biogeography of Bahamian *Cerion* for more than a decade (see literature cited) and have been able to refute these two myths by systematic revision and synonymization of invalid taxa. In our simplified system of biological taxa mapped and studied in the field, the chaos of traditional names breaks down to be replaced by clear order and stable pattern, temporally and spatially, in the distribution of Bahamian *Cerion* among islands.

We have detected order at two basic levels of variation, and have portrayed this coherence primarily by the study of covariance sets, or groups of characters correlated by the general geometries of snail growth and the particular allometries of *Cerion*. We find, first, sensible order within taxa, based upon clines defined geographically (Gould and Paull, 1977 for *C. striatellum*) or ecologically (Gould and Woodruff, 1986 on dwarfing in *C. gubernatorium*), or upon small-scale but discontinuous differentiation among islands (Gould and Woodruff, 1978 on *C. bendalli* in Abaco and Grand Bahama; Gould, 1984a on *C. uva* in Aruba, Bonaire and Curaçao). Second, we have demonstrated consistency in the distribution and interaction of taxa within regions. We find the same forms (or "morphotypes," for we do not know their genealogies) in the same settings from island to island within regions ("ribby" *Cerion* on bank-edge coasts, and "mottled" *Cerion* on bank-interior coasts and island interiors on all major islands of the northern Bahamas, Gould and Woodruff, 1978, 1986). When anomalous taxa invade regions, they occupy restricted areas superimposed upon the underlying predictability of indigenous forms (for example, incursions of the subgenus *C.* (*Umbonis*) into bounded portions of the "ribby" coastal range on eastern Andros, Cat and Long Islands).

II. A Strategy of Research

We have reached the half-way point in our systematic and evolutionary revision of Bahamian *Cerion*. We have studied all major islands of the northern Bahamas (Little and Great Bahama Bank) and have found on each of the eight primary territories (Grand Bahama, Abaco, Andros, New Providence, Eleuthera, Cat, Exuma, and Long Island) the same basic distribution of bank-edge (usually east coast)

"ribby" and bank-interior (usually west coast) "mottled" *Cerion* described above (see Gould and Woodruff, 1986 for summary). In addition, at least two islands (Cat and Eleuthera) harbor relict populations of the major Sangamon taxon from the ca. 120,000 year b.p. dunes of these islands—smooth, white, thick-lipped *C. agassizi*. Finally, a few local incursions of other taxa, usually of the subgenus *C.* (*Umbonis*), have been recorded. The identification of this consistent pattern has permitted us to reduce the bloated taxonomy of Bahamian *Cerion* by more than half, synonymizing some 300 invalid names to a half-dozen or so biological species.

We now extend this program to the genuinely different *Cerion* faunas of the southeastern Bahamas (Inagua, Mayaguana, Crooked-Acklins, and the geographically linked though politically independent Turks and Caicos). The major difference between the two regions is evident by inspection of museum collections. Whereas the ribby-mottled distinction unlocks the northern Bahamas, the main *Cerion* morphotype of the southern Bahamas is an ovate-triangular, generally smooth and white form known by a plethora of names—*C. columna* and *C. christophei* on Inagua, *C. regium* on Castle Island, *C. piratarum* on Mayaguana, *C. regina* on Grand Turk, *C. caicosense* on South Caicos, for example—but sufficiently similar from place to place to provoke a strong suspicion that their underlying unity might provide a key to the southern region. This study is a first attempt to apply the methods that we used successfully in the northern Bahamas to the different fauna of the southern islands, in particular to variation within the "tapering" morphotype (as we shall call it).

We choose the Turks and Caicos islands for this first attempt for two reasons. First, these banks are, geographically speaking, the eastern outliers of the Bahamian complex. Their *Cerion* faunas are simpler than those of larger, more central islands like Inagua. We have had success in our previous work by beginning with sparser faunas of peripheral areas (Gould and Paull, 1977; Gould, 1969a, 1984a) and working towards greater, central complexity (Gould and Woodruff, 1986). Second, several names have been applied on various islands of the Turks and Caicos to populations that may all belong to the tapering morphotype. If we can resolve the current set of unrelated names into a pattern of coherent variation, then we may hope that the southern Bahamas will also yield to a replacement of taxonomic chaos by biological order. In this case, a revision of the entire Bahamian *Cerion* fauna will be within our grasp.

III. The Current Status of the Turks and Caicos *Cerion* Fauna

The available nomenclature for Turks and Caicos *Cerion* provides an excellent example of the systematic problem (systematic, that is, in both technical and vernacular senses) besetting this genus. The Turks and Caicos, spared visits by the most ardent splitters among *Cerion* aficionados, are relatively "underrepresented" by *Cerion* species. Clench's (1957) catalogue lists nine taxa, and two have been added since (Clench, 1961). The existing descriptions give no hint of any order or pattern in the distribution of these supposed taxa on the various islands.

The first eight names were bestowed by Pilsbry and Vanatta in their short paper of 1895 and their catalogue of 1896. Pilsbry, impressed by Maynard's demonstration that the internal teeth and lamellae of *Cerion* shells had taxonomic value, engaged Vanatta to section shells in the extensive collection of the Academy of Natural Sciences of Philadelphia. He thought, in so doing, that he had "brought to light" many new species. In particular, he distinguished for the first time a "Turk's Island" (1895, p. 208) species of *Cerion* from other taxa of the tapering morphotype. He named this first Turks and Caicos species *C. regina* (1895, p. 208), distinguishing it from *C. columna* of Inagua by its more

triangular profile (*C. columna*, as its name implies, is more parallel-sided); from *C. regium* of Castle Island by its smaller size and less thickened apertural lip (as compared with the thick lip of *C. regium*, described in a disparaging and mildly racist manner by Pilsbry and Vanatta as "a lip of quite Ethiopian characteristics"); and from *C. lentiginosum* and *C. album* of Rum Cay by its smoother shell (for the Rum Cay species are costate on their early whorls). Pilsbry and Vanatta then named five subspecies of *C. regina*, in order (pp. 208–209) as *C. r. percostatum* for ribbed shells; *C. r. comes* (literally, the pretty queen) for shells "heavily streaked and blotched with chestnut brown"; *C. r. Swiftii* for smaller, thinner and more triangular shells; *C. r. eucosmium* for smooth, glossy shells with livid, pinkish-brown streaks; and *C. r. brevispira* for short, compact shells. All these names were applied to shells from "Turk's Island," presumably Grand Turk of modern nomenclature. All names refer to common variants of color, ribbing, and size (with engendered covariances in shape) now recognized as the major and pervasive paths of variation throughout the genus.

Pilsbry and Vanatta then recognized a second species from "Turk's Island" as *Cerion incanoides* (1895, p. 209). They noted that "this species belongs clearly to the group of *C. regina*, *lentiginosum*, etc." (loc. cit.), but established a separate taxon to recognize the thin and smooth shell of this form. We do not understand why they made this distinction because, at least to us, collections of *C. incanoides* differ no more from *C. regina* than do several of the *C. regina* subspecies among themselves.

In their 1896 catalogue, a landmark attempt to systematize the entire genus, Pilsbry and Vanatta listed the Turks and Caicos taxa included under and allied with *Cerion regina*. They then named, as *C. blandi* (1896, listed on p. 324, described on p. 334), a genuinely different *Cerion* from this region. They included this thick and solid, small to medium sized, cylindrical rather than triangularly shaped, and strongly ribbed shell in the group of *Cerion glans*, the typical ribby *Cerion* of the northern Bahamas. In so doing, they made an interesting error. *C. blandi*, confined to small Salt Cay of the Turks group, represents an incursion of the distinctive subgenus *C.* (*Umbonis*) that has hybridized to varying degrees with *C. regina* stocks. *C.* (*Umbonis*) has distinctively wavy ribs and incised spiral lines, but these characters are often muted in hybrid forms. In particular, as in *C. felis* of Cat Island and *C. glans irregulare* of northern Andros (both hybrids between an umbonid and *C. glans*), most specimens lack the incised lines and bear strong ribs only moderately wavy. In this "diluted" state, shells of *C. blandi* do superficially resemble standard ribby *Cerion*. Indeed, Pilsbry and Vanatta glimpsed the true status of *C. blandi* in adding to the end of the description: "but the ribs are conspicuously different, peculiarly rough and unfinished, somewhat like *C. felis*" (1896, p. 334). *C. felis* is a *C.* (*Umbonis*) hybrid from Cat Island.

In 1937, Clench described the first *Cerion* from the Caicos islands, establishing the new species, *C. caicosense*. Clench recognized its allegiance with *C. incanoides* and the *C. regina* group, but felt that smaller size, whiter color, and proportions of the apertural teeth (parietal smaller and columellar longer) warranted a new species. We shall show that the Caicos populations, particularly from South Caicos, are distinct biometrically, but for none of the reasons identified by Clench, since all his differentia show overlap with mean values from Turks island populations.

In 1961, Clench wrote a summary paper on land shells of the Turks and Caicos. He properly lumped all previous names for the *C. regina* group, except his own *C. caicosense*, into *C. regina* itself (1961, p. 250), not primarily for morphological reasons, but because all had been described from Grand Turk, and the necessary criterion of geographic distinction for subspecies had not therefore been met. He

retained *C. caicosense* primarily for its geographic separation.

Clench then added two new taxa. First, he described as *C. utowana abbotti* (1961, p. 251) shells from several islands on both Turks and Caicos banks that differed from *C. regina* primarily in the parallel-sided, rather than tapering form of the adult shell. This decision baffles us for two reasons. First, we do not know why he designated these shells as a subspecies of the East Plana Cay form *C. utowana* since its relationships, to us at least, seem so clearly with the local *C. regina* forms. Our biometric work, based on characters that Clench used to distinguish this taxon, places these populations squarely within the *C. regina* field (see section VI C). Second, we do not understand why he distinguished this taxon at all since several populations within *C. regina* share this morphospace in the common continuum from quite triangular to quite cylindrical shells.

Clench then designated as *C. lewisi* (1961, p. 255) an uncontestably different *Cerion* from several islands in the northwestern Caicos. This very thin, strongly mottled, cylindrical, smooth shell looks nothing like any other Turks and Caicos *Cerion*, yet cannot be distinguished conchologically from the highly distinctive *C. lepidum* from nearby parts of Cuba. We do not doubt, as Clench also concluded, that *C. lewisi* is a Cuban emigrant restricted to a few islands of the Caicos Bank.

The existing taxonomy therefore leaves us confused. *C. blandi* (an umbonid incursion probably phasing itself out by hybridization), and *C. lewisi* (a Cuban emigré) are distinct and locally restricted products of probably recent immigration. The prevalent local form, the tapering morphotype that gives the southern Bahamas its *Cerion* "signature," now carries four species names of uncertain status. Pilsbry and Vanatta's *C. regina* has priority, but *C. incanoides* (though synonymized with *C. regina* by Clench) also refers to Turk Island forms. *C. caicosense* has been applied to Caicos island populations, but the basis of its distinction remains unclear. Finally, *C. utowana abbotti* has been described from both banks, but with no evident differences from the *C. regina* incumbents. Moreover, no one has ever claimed any consistent or simplifying pattern in the geographic distribution of the *C. regina* complex in the Turks and Caicos islands. A resolution of *Cerion* on these banks must evidently center on a proper characterization and mapping of morphological differences within the *C. regina* group.

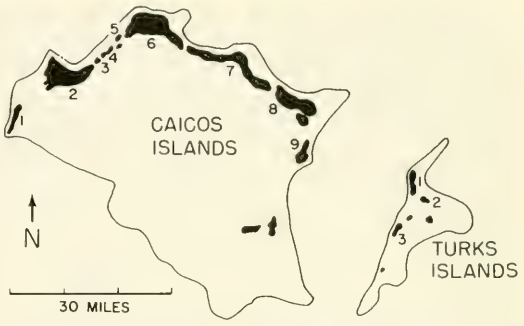

Figure 1. Islands of the Turks and Caicos banks. Turks: 1, Grand Turk. 2, Long Cay. 3, Salt Cay. Caicos: 1, West Caicos. 2, Providenciales. 3, Pine Cay. 4, Water Cay. 5, Parrot Cay. 6, North Caicos. 7, Grand Caicos. 8, East Caicos. 9, South Caicos.

IV. Materials and Methods

We have based our systematic revisions of *Cerion* on biometric and genetic studies of animals collected personally in the field as we map the ecologic and biogeographic distribution of *Cerion*. (We have often, as here, augmented our own material with samples from Museum collections representing populations no longer extant or difficult of access.) In May–June, 1978, we visited the Turks and Caicos to study the geographic and ecological distribution of variation in the tapering morphotype. We collected extensively on South Caicos, sampling every population that we could locate; we then sampled less fully on the largest and most distant island of the Caicos Bank (Providenciales), and on the major island of the Turks Bank (Grand Turk).

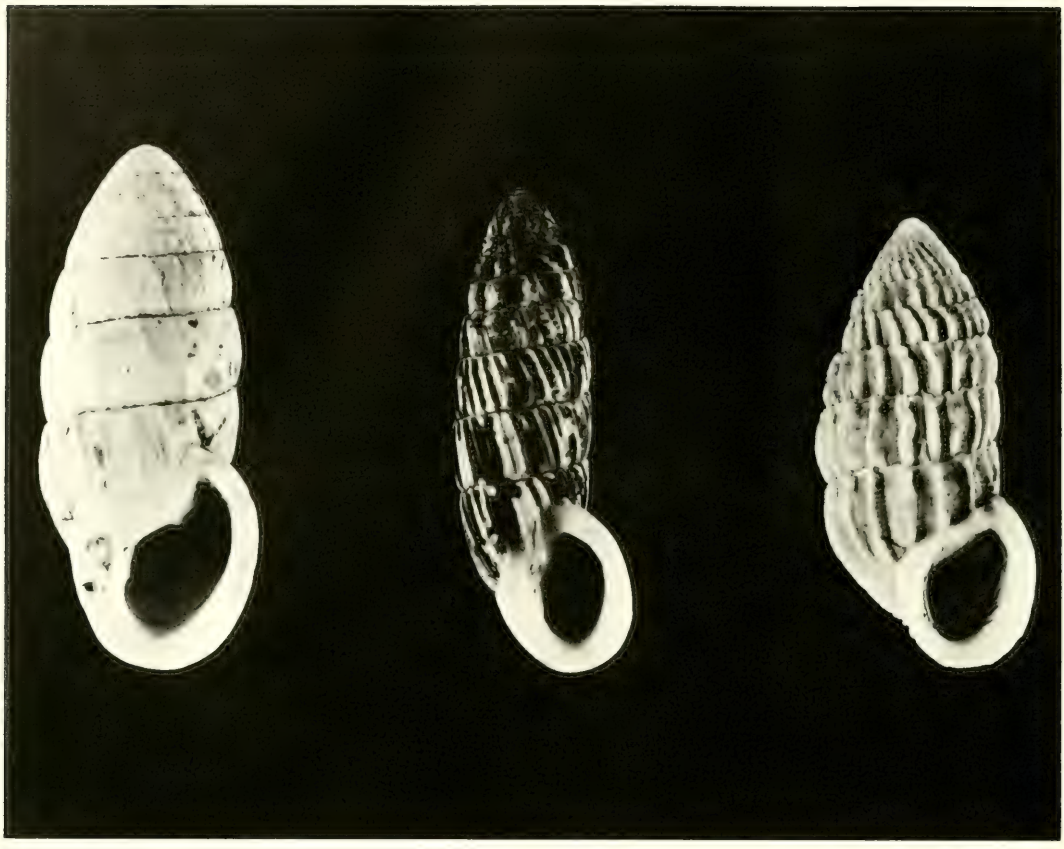

Figure 2. Representative specimens of the three *Cerion* taxa of the Turks and Caicos. Left, *C. regina* from South Caicos, our sample 753. Middle, *C. lewisi* from Parrot Cay, Caicos Bank, MCZ No. 221566. Right, *C. blandi* from Salt Cay, Turks Bank, MCZ No. 220913. Note characteristic *C.* (*Umbonis*) features of *C. blandi*: wavy ribs and incised lines perpendicular to the ribs. The *C. regina* specimen is 34.0 mm high.

We used 29 of our own samples for our morphometric analysis, 23 living and six subfossil. These include 19 from South Caicos (14 living, five subfossil), seven from Grand Turk (six living and one subfossil), and three from Providenciales (all living).

We then selected 32 additional samples for biometric analysis from the collections of the Department of Mollusks at the Museum of Comparative Zoology. These include 15 samples of the tapering morphotype (13 from islands that we had not visited, and two from South Caicos—the paratypes of *C. caicosense*, and *C. utowana abbotti*, both taxa that we regarded as ripe for synonymy). In addition, we measured ten samples of *C. blandi* and its hybrids with tapering forms, all from Salt Cay on the Turks Bank, and seven samples of *C. lewisi* from the western Caicos (West Caicos, Providenciales, Pine Cay, Water Cay, Parrot Cay and Ft. George's Cay). Thus, our set of 62 samples represents all taxa (including types and paratypes, where available), on all islands of their recorded and available distribution. Samples are listed individually in the appendix with their field or museum numbers and their location. Figure 1 shows the islands of both banks, while Figures 2 and 3 display the range of form within the Turks and Caicos *Cerion* fauna (Fig. 2 the contrast among

Figure 3. Representative specimens for variation within *C. regina.* Top row, the three islands represented in our personal collections. Left, South Caicos from sample 753. Note the relatively squatter apex—the key defining feature of South Caicos populations. Middle, more apically pointed, finely ribbed and mottled specimen from Providenciales, sample 771. Right, large and apically pointed specimen from Grand Turk, sample 781. Bottom row, representative specimens from paratype samples of two other designated species from South Caicos, both in our view synonyms of *C. regina.* Left, *C. caicosense.* Right, *C. utowana abbotti.* The upper row left specimen is 33.5 mm high.

the three recognized taxa; Fig. 3 the range of variation within the tapering morphotype, here treated as a single species *C. regina*).

For the biometric analysis, we selected 20 adult specimens at random from each sample and measured, for each shell, 18 characters and four additional derived ratios; this study therefore rests upon more than 20,000 direct measurements upon some 1,200 specimens in 61 samples. We have followed the protocol for measurement and analysis used in our recent work (especially Gould and Woodruff, 1986, explained more fully in Gould and Woodruff, 1978), and will not repeat the details here. Table 1 describes and lists the characters, and Figure 4 displays the points for measurements of the aperture and last whorl. The 22 measures used here include 19 of our previous set of 21 (excluding number of ribs on the 4th and 6th whorls because smooth shells of the tapering morphotype lose their juvenile ribs by this stage), plus three basic indices of shell shape (height to width ratios of the protoconch, of the final adult shell, and at the end of the fourth postprotoconch whorl) found

TABLE 1. BRIEF DESCRIPTION OF MEASURES USED IN THIS STUDY (GIVEN IN ORDER OF ARRAY IN SUBSEQUENT TABLES).

1. PROWID	Width of the protoconch
2. FOURWID	Width of shell at the end of the fourth whorl
3. NUMWHO	Total number of whorls, counting from the end of the protoconch as zero
4. RIBDENS	Number of ribs in 50 micrometer units at the end of post protoconch whorl 1
5. LENGTH	Total length of the shell
6. WIDTH	Total width of the shell
7. PROHT	Height of the protoconch
8. FOURHT	Height of shell at the end of the fourth whorl
9. FRSXHT	Height of shell from the end of the fourth to the end of the sixth whorl
10. UMBWID	Maximum width of the umbilicus
11. LIPWID	Maximum width of the lip
12. LIPTHK	Maximum thickness of the lip
13. APHT	Height of the aperture AB′ of Fig. 4
14. APWID	Width of the aperture C′D of Fig. 4
15. APROT	Projecture of apertural lip beyond outline of previous whorls, C″D of Fig. 4
16. EC	Distance from last suture to umbilical border of aperture, measured perpendicular to the suture, EC of Fig. 4
17. FA	Distance from last suture to parietal border of aperture, measured perpendicular to the suture, FA of Fig. 4
18. APTILT	The ratio EC/FA, a measure of the tilt of the aperture
19. WEIGHT	Weight of the shell
20. HWRATIO	The ratio of height to width of the shell, measures 4/5
21. PRORAT	Width/height ratio of the protoconch, measures 1/7
22. FOURRAT	Width/height ratio of the shell at the end of the fourth whorl, measures 2/8

useful in our study of sinistral *Cerion* (Gould, Young and Kasson, 1985). The mean values for all measures in all samples are given in the appendix.

Our measures are chosen to record the major shell characters used to make taxonomic distinctions, including sizes and shapes of protoconch, adult shell, and intermediate whorls; size, form and orientation of the aperture and umbilicus; ribbing and shell thickness; and size and form of the apertural lip. We have also included measures that will permit a reconstruction of basic coiling geometries, following both the analytical schemes of Raup (1966, for example) and the actual, more complex allometries of *Cerion*. *Cerion* is a nearly ideal animal for biometric research. The transition from protoconch to later growth is clearly marked, providing a clear and natural criterion for numbering whorls. Unlike most mollusks, *Cerion* possesses a definitive adult form; as growth reaches its termination, the direction of coiling shifts, the shell overgrows its previous whorls slightly, and then deposits an expanded and thickened adult lip, ceasing all growth thereafter. Thus, we can measure the adult size of *Cerion* shells, without confounding ontogenetic and static variation—a primary source of confusion in most biometric studies of snails.

Two aspects of our research program suggest a factor analytic approach as most appropriate for our analysis: first, because we wish to explore the distribution of samples in the general *Cerion* morphospace (rather than trying to test distinctions, taxonomic or otherwise, previously proposed); second, because our primary interest in the inductive study of morphology centers upon covariance sets, or groups of associated characters often flagged so well by various rotations of factor axes.

Consequently, we have portrayed each sample by its vector of means (see appendix), submitted these vectors to transformations that weight characters equally (percent-range), normalized the vectors to equal length (so that allometric effects will be expressed as shape and simple size difference will not swamp more subtle associations), and then performed our factor analyses on the transformed matrix of mean vectors. (Our analyses are in the less usual, or "inverted," Q-mode format, with loadings as samples and scores as variables, rather than in the more conventional

R-mode—see justification and empirical demonstration of equivalency between the modes in Gould and Woodruff, 1978, 1986.)

The problems presented by variation among *Cerion* samples of the Turks and Caicos may be conceptualized as a descending series of levels, each posing different questions and capturing different information. First, the positioning of all samples in a general morphospace to demonstrate the role of historical contingency in shaping the fauna by bringing two allochthones (the umbonid *C. blandi* and the Cuban import *C. lewisi*) into primary territory of the tapering morphotype. Second, the positioning of tapering samples within the morphospace set by the tapering morphotype itself to see whether any simplification of pattern might replace the current, chaotic taxonomy. Third, the positioning of samples from South Caicos alone within their own morphospace to explore, for our best and most abundantly sampled island, any order in local variation that would probably be swamped by inter-island and inter-taxon effects at the higher two levels. Fourth, and finally, the ordering of specimens within samples (this last being, of course, a break with, rather than a smooth descent from, the previous three levels, since it treats within-sample variation of specimens rather than between-sample variation of mean vectors).

We are interested not only in relationships among objects (as discussed above) but also in the associations of variables that build major dimensions of the morphospace, for the covariance sets thus defined act as constraining channels of variation that both limit the kinds of variation expressed, and also provide opportunity for generating large and diverse changes of form from small inputs (via correlated consequences). The tension between these superficially contradictory but linked themes of limitation and amplification defines *Cerion*'s major interest to students of morphology.

We complemented the biometric study with a survey of genetic variation in snails

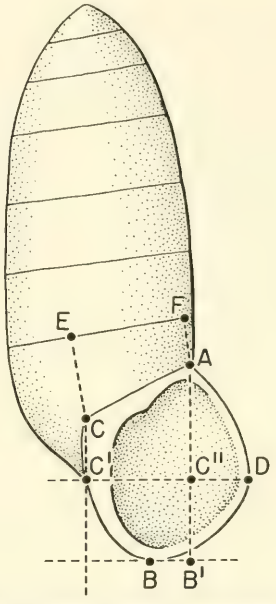

Figure 4. Sketch showing points that define our measures of the aperture. See Table 1.

of the tapering morphotype. Our survey involved more than 520 individual adult snails representing 16 populations distributed among the islands as follows: Providenciales: 2, South Caicos: 13, Grand Turk: 1. One population from South Caicos (site 758) was represented by two subsamples: 758T from a single coconut palm tree and 758 from the surrounding grass and shrubs. In most cases the same individual animals were used for both conchological and genetic study. All samples were taken by searching an area of typically 10 m^2 (a fraction of the neighborhood size) and collecting every adult encountered.

Genetic characterization was based on an examination of individual variation in 16 proteins (Table 2) extracted from foot-muscle tissue. Variation was detected by horizontal starch gel electrophoresis under conditions we have described elsewhere (Gould and Woodruff, 1986; Woodruff, 1975). Using the BIOSYS-1 computer program (Swofford and Selander, 1981) we calculated allele frequencies for each sample together with measures of genetic variation including mean number of alleles per

Table 2. Enzyme systems analyzed in Turks and Caicos *Cerion*.

Protein name (E.C. Number)	Abbreviation	Loci	Conditions*
Aspartate aminotransferase (2.6.1.1)	*Aat*	1	A
Ceruloplasmin	*Crp*	1	A
Esterase α-naphthyl acetate (3.1.1.1)	*Es*	3	B
General protein	*Pr*	1	B
Glucose phosphate isomerase (5.3.1.9)	*Gpi*	1	B
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	*Gapd*	1	A
Lactate dehydrogenase (1.1.1.27)	*Ldh*	2	A
Malate dehydrogenase (1.1.1.37)	*Mdh*	2	B
Phosphoglucomutase (2.7.5.1)	*Pgm*	2	B
6-Phosphogluconate dehydrogenase (1.1.1.44)	*6pgd*	1	B
Superoxide dismutase (1.15.1.1)	*Sod*	1	A

* Electrophoretic conditions: A = tris borate EDTA buffer, pH 8.6, 250 volts, 4 hrs; B = tris citrate buffer, pH 6.7, 159 v, 4 hrs.

locus ($\bar{A}$), proportion of polymorphic loci (P), and mean individual heterozygosity by direct count ($\bar{H}$). We performed χ^2 goodness-of-fit tests and also calculated exact probabilities to test for random mating. Wright's (1978) F-statistics were used to assess the extent of genetic differentiation within and between samples and also to test for panmixia. Nei's (1978) unbiased measures of genetic identity (I) and genetic distance (D) were calculated for all pairwise comparisons of samples.

V. Covariance at Level One: The General Pattern

In Figure 5, we plot the loadings of all 55 modern samples (excluding only the six fossil samples) on the first three axes (93.7% of all information) of a varimax rotation for a factor analysis of the matrix of mean vectors. (In this triangular plot, the three loadings for each sample are normalized to a sum of 1.0, thus providing a representation of three dimensions in two, with axes at each corner of the triangle. All but one sample have communalities above 0.87, and this procedure introduces very little distortion of relationships among samples. The strongly dwarfed tapering sample from Sand Cay is the sole exception, with a communality of 0.36; nearly all its remaining information lies on a fourth axis defining it alone.)

The evident order of morphological distribution among samples emerges as a pleasing first result; the lack of pattern in existing taxonomies is, as we had predicted and as we have found in all our *Cerion* work elsewhere, an artifact of definition. The three axes are foci for the three major kinds of *Cerion* on the Turks and Caicos—the indigenous tapering morphotype and the two localized immigrants, *C. blandi* and *C. lewisi*. The most distinctive form, pencil-thin and strongly mottled *C. lewisi*, defines the second axis, and all its samples cluster in a small space of high values. The first axis is a referent for tapering samples, and we can already discern clear order in geographic clustering among islands (discussed fully in the next section on the morphospace of tapering samples alone). In particular, all samples from South Caicos occupy a small, unique field nearest the first axis. *C. blandi* occupies a broader field, high on the third axis, overlapping slightly with samples of the tapering morphotype (with which it hybridizes).

The matrix of factor scores (Table 3) defines the bases for distinctions on these axes. When we consider such covariances for a matrix of samples from a single morphotype generated by a single pattern of growth (see next section), then associations of variables tend to record pathways and constraints of development, and factor

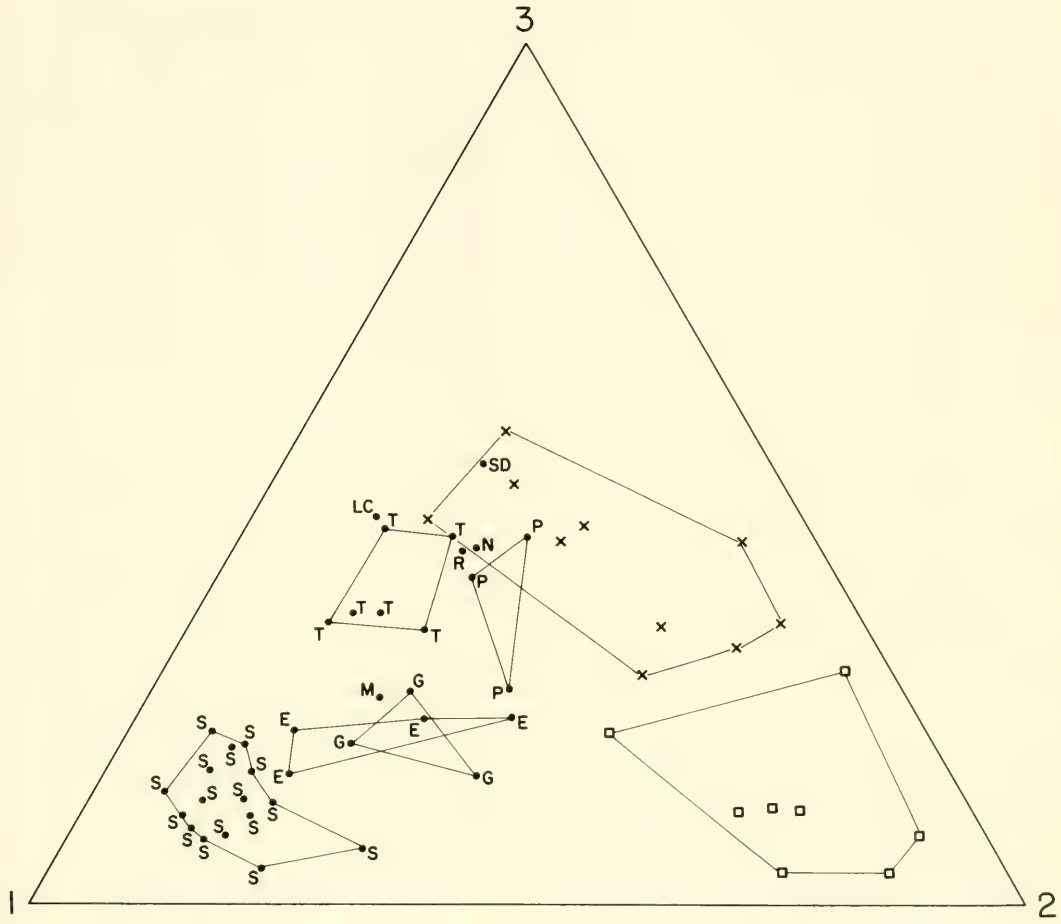

Figure 5. Normalized factor loadings of mean vectors for all nonfossil samples upon the first three varimax axes. Crosses are *C. blandi*, squares *C. lewisi*, and dots *C. regina*. Island for *C. regina* identified as: S, South Caicos; E, East Caicos; M, "Middle" Caicos; N, North Caicos; G, Grand Caicos; P, Providenciales; T, Grand Turk; LC, Long Cay of Turks Bank; SD, Sand Cay of Turks Bank; R, island unknown. Convex polygons are drawn around all samples of *C. lewisi*, *C. blandi*, and *C. regina* from South Caicos, East Caicos, Grand Caicos, Providenciales, and Grand Turk.

analysis becomes a chief tool in the inductive study of constraints and adaptation. But variation lies at too high a level for such an interpretation here because the differences "picked out" by the axes are not dimensions of growth within a coherent form, but the differentia of taxonomic entities forced into the same analysis only by historical contingencies of immigration. Thus, the factor scores of this analysis are records of the basic morphological separation among taxa haphazardly assembled by nature.

The high scores on the second axis all record the chief distinguishing features of its focal cluster, *C. lewisi*—the coordinated characters of a very slender shell achieved by growing many whorls of normal size, not by whorls of unusual height. The shell begins high (0.349 for protoconch height), but height of later whorls do not score strongly. The most distinctive character of slimness (height/width of adult shell at 0.569) is achieved by growing a large number of whorls (0.413), an efficient path to relative narrowness since

TABLE 3. FACTOR SCORES FOR THREE-AXIS SOLUTION (93.7% OF INFORMATION) FOR ALL NONFOSSIL SAMPLES.

	Measure	Axis 1	Axis 2	Axis 3
1.	PROWID	0.124	0.076	0.141
2.	FOURWID	0.269	−0.157	0.265
3.	NUMWHO	0.055	0.413	−0.048
4.	RIBDENS	−0.093	0.407	0.105
5.	LENGTH	0.182	0.233	0.056
6.	WIDTH	0.211	−0.079	0.229
7.	PROHT	−0.294	0.349	0.493
8.	FOURHT	−0.058	−0.030	0.489
9.	FRSXHT	0.282	−0.061	0.191
10.	UMBWID	0.119	−0.050	0.391
11.	LIPWID	0.177	0.046	0.074
12.	LIPTHK	0.249	0.020	−0.059
13.	APHT	0.230	0.040	0.059
14.	APWID	0.253	−0.013	0.037
15.	APROT	0.143	0.067	0.129
16.	EC	0.236	0.135	−0.022
17.	FA	0.171	0.273	0.051
18.	APTILT	0.084	0.092	0.032
19.	WEIGHT	0.138	−0.027	0.178
20.	HWRATIO	0.030	0.569	−0.212
21.	PRORAT	0.414	0.086	−0.222
22.	FOURRAT	0.353	−0.051	−0.097

the standard allometry of *Cerion* adds height but little or no width throughout middle to late growth (see Gould, 1984b). The numerous fine ribs of this species also distinguish this taxon (0.407) from all other Turks and Caicos *Cerion*.

The third axis, focus for *C. blandi*, records its highest scores for characters well known (see Clench and Aguayo, 1952) as distinct features of its peculiar subgenus *C.* (*Umbonis*)—a wide umbilicus (0.391) and high early heights (0.493 for the protoconch, 0.489 at the end of the fourth whorl). *C.* (*Umbonis*) grows a thin, tapering triangular top by rapid excursion in height, however much the shell may broaden out later in ontogeny.

Scores on the first axis, focus for tapering samples, are more complex because they record two distinct sources of variation—first, a basis of separation between tapering samples and the other two taxa; and, second, the major source of geographic division within tapering samples (note the contrast of South Caicos samples with all others). For the first source, tapering samples are most evidently distinct from other taxa by their generally larger shell size. We find this size difference recorded in the usual manner of factor analytic studies (see Jolicoeur, 1963, 1984)—fairly low and uniform values (averaging about 0.2 in this case) for all measures of basic dimensions in the adult shell (length, width, aperture length and width, sizes of last whorls, that is, measures 5, 6 and 13–17). Standardized sizes of late whorls (fourth width at 0.269, and fourth to sixth height at 0.282) also covary with final sizes.

However, since South Caicos samples load most highly on this axis, we find in addition to these low and uniform scores for general size a few higher scores for distinctive South Caicos characters (see next section), particularly the high values (0.414 and 0.353) for early shell shape (width/height ratios of protoconch and fourth whorl). The relatively flat apices (rapid early growth in width unmatched by height) of South Caicos tapering samples are their chief distinguishing character, both visually and biometrically (see appendix).

VI. Genetics and Morphometrics at Level Two: A Taxonomic Resolution of the Tapering Morphotype

A) The General Pattern: Resolution of Outliers

Figure 6 is a triangular plot of mean vectors for tapering samples alone in their own morphospace. Each island occupies a restricted field arrayed between the first two axes, thus affirming the most important conclusion that we have reached, in study after study, of geographic variation within *Cerion* taxa (Gould, 1984a; Gould and Woodruff, 1978 for example): geographic coherence of shell form marks all *Cerion* distributions; the signature of places is never obliterated.

The array contains an outlier, the strongly dwarfed population from Sand Cay, Turks Bank. Its distinctness is exag-

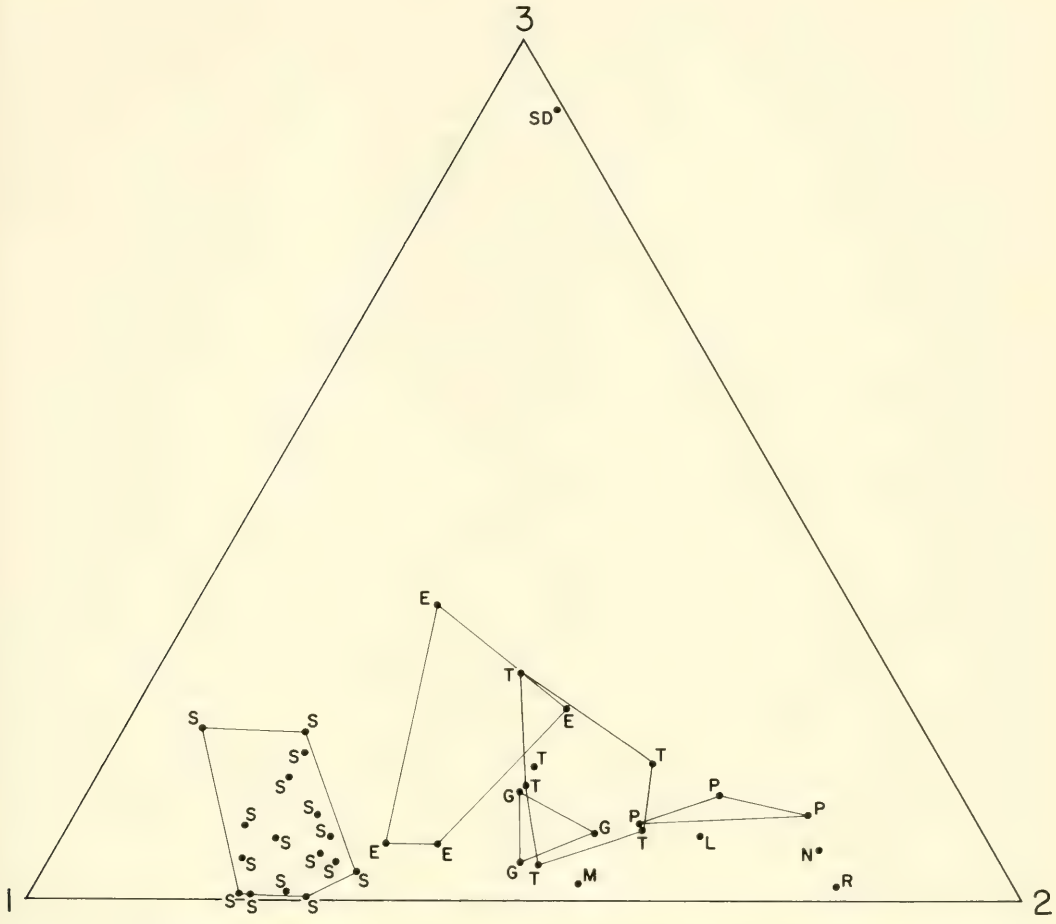

Figure 6. Normalized factor loadings for *C. regina* samples only. Symbols as in Figure 5.

gerated in Figure 6 because factor analysis in varimax rotation tends to absorb uniquenesses on separate axes. The distinctive features of Sand Cay are abstracted by this axis; when plotted into morphospaces that do not include this dimension (as in Fig. 1), Sand Cay plots near all other populations of the tapering morphotype on Turks Bank.

The designation of Sand Cay's uniqueness by an entire axis compresses all other variation into the smaller space of two dimensions. Thus, to expand the portrayal of normal-sized samples in the tapering morphotype, we eliminated the Sand Cay population and repeated the analysis, plotting the triangular diagram as Figure 7. Note that the ordering of normal-sized samples is thereby spread out, but not in any way altered (compare Figs. 6 and 7). The basically linear array of South Caicos-East Caicos-Grand Caicos-Providenciales remains. This array is compressed into two axes on Figure 6, but expanded to three in Figure 7, as the sequence remains fixed in second axis projections, while *each island* now spreads out along the domains of axis one and three.

The Sand Cay population bears, by Clench's own decision (as curator of Mollusks at the Museum of Comparative Zoology), the name *C. utowana abbotti*, one

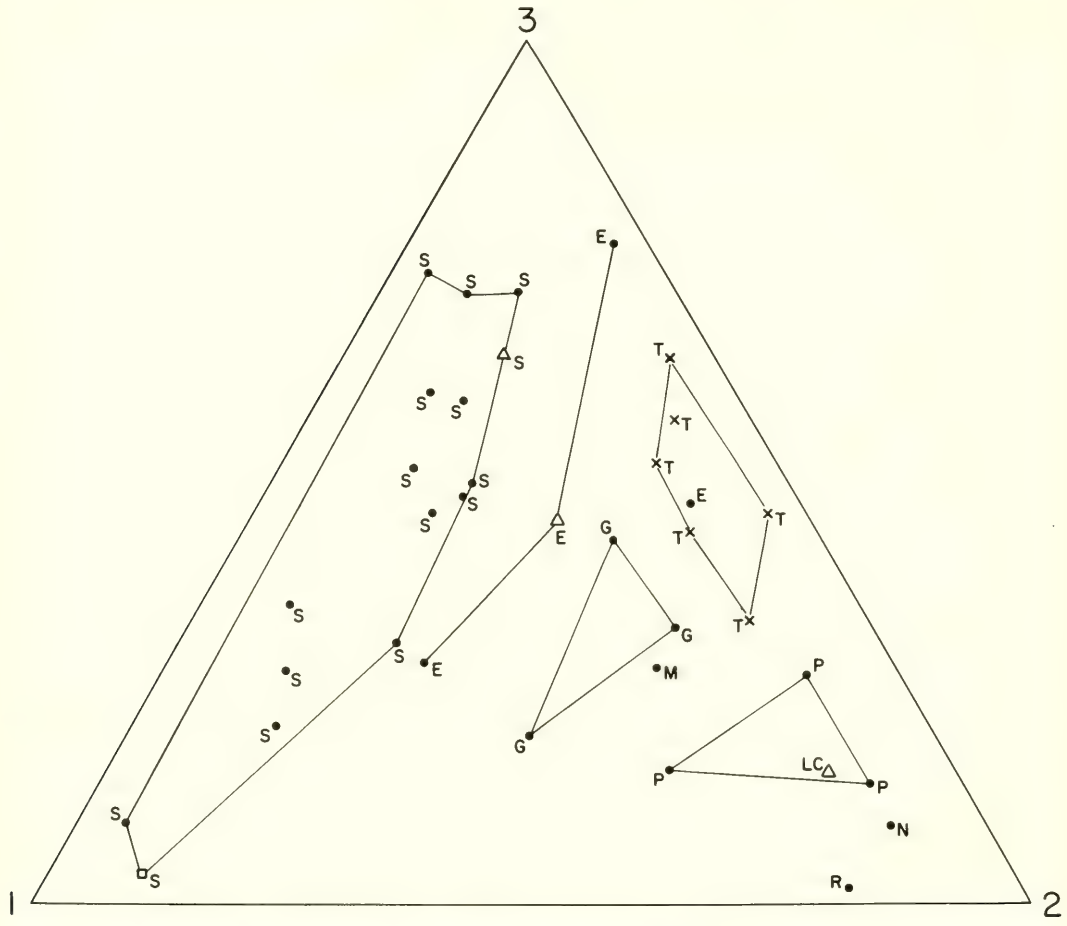

Figure 7. Normalized factor loadings for all *C. regina* samples excluding the Sand Cay dwarfs. Open triangles are samples designated *C. utowana abbotti* by Clench. The open square is the paratype sample of *C. caicosense*.

of the disputed taxa within the tapering morphotype—so one might suspect the validity of this taxon on morphological grounds. But three other samples designated by Clench as *C. utowana abbotti*, including the paratypes from South Caicos, plot (as we shall discuss in part C of this section) at expected positions for their islands within the tapering morphospace. Sand Cay's uniqueness is a consequence of its dwarfing—a simple alteration that provokes, via *Cerion*'s allometries, a large suite of complex changes producing a large overall excursion for the morphological vector considered in toto (see Gould, 1984b; Gould and Woodruff, 1986 for other morphometric analyses of dwarfing in *Cerion*).

The Sand Cay population is not the only strongly dwarfed sample of the tapering morphotype. A subfossil sample from South Caicos (765) yields an even more distant outlier attributable to dwarfing; (see Fig. 8 on the representation of all samples, including the subfossils. Note that axes two and three are reversed relative to Fig. 5, but that the ordering of samples and clusters is not altered). Note that the subfossil

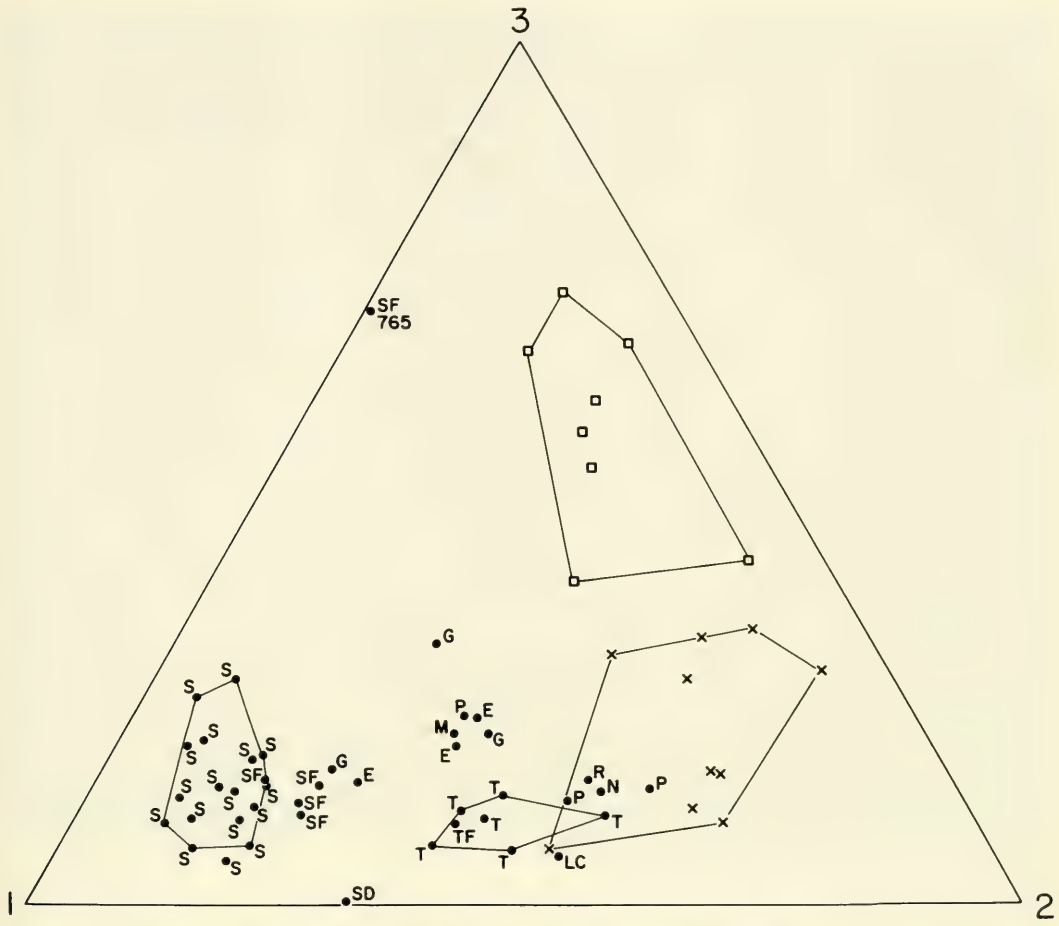

Figure 8. Normalized factor loadings for all samples, now including fossils. Symbols as on Figure 5 with the following additions for fossils. SF, South Caicos fossils (note their position adjacent to but outside the polygon of modern South Caicos samples); TF, Grand Turk fossils; and SF765, smokestack dwarf fossils from South Caicos.

and Sand Cay dwarfs occupy outlying positions at the *opposite* ends of third axis projections.

Fortunately, as the result of a prior study in *Cerion*'s dwarfing (Gould, 1984b), we can identify the common basis in growth and allometry of these apparently contradictory morphological excursions in the two dwarfed populations (see Gould, 1984b). Axis three is the focus in Figure 8 for pencil-thin *Cerion lewisi*. The subfossil dwarfs, projecting as strongly on the third axis as any *C. lewisi* sample, are verging towards "smokestacks" in the terminology of Gould (1984b)—that is, they become dwarfed by restricting whorl size while growing a normal number of whorls. Since *Cerion* increases in height but not in width as later whorls are deposited, this style of dwarfing adds height for a usual amount of coiling to the narrow base of dwarfed whorl size, producing a slender shell. But the Sand Cay dwarfs are "double whammies"—that is, dwarfs through the twin action of reduced whorl size *and* decreased whorl number, leading to squatter than average

Figure 9. Two distinct styles of dwarfing in *C. regina,* producing the major outliers in this species. Left: two specimens from sample 765, South Caicos. Note relative thinning of these smokestack dwarfs with respect to the normal (central) specimen from sample 756, South Caicos. Right: two specimens of Sand Cay dwarfs. Note relatively squatter shells of these "double whammy" dwarfs compared with normal specimen. Leftmost dwarf is 19.1 mm high. Central specimen is 34.9 mm high.

shells through the suppression of whorls that would add height without width. They therefore plot at the opposite end of axis 3, the focus for high-spired *C. lewisi.* This structural understanding of dwarfing and its allometries resolves two issues: first, we can interpret two apparently opposite directions of morphological change as different consequences of the same triggering phenomenon; second, we can accommodate two outlying samples as resolvable expressions of the tapering morphotype, not as taxonomic anomalies. Figure 9 portrays the unusual morphologies of the two dwarfs. Note also (see appendix for more details), the key mean values in the two dwarfed samples for this interpretation. The subfossil smokestack has (at 2.70) the third largest height/width ratio among South Caicos samples, and (at 7.2) a mean whorl number only slightly below average. The Sand Cay "double whammy" has (at 2.20) by far the squattest shell of Turks Island forms, and (at 6.6) by far the smallest number of whorls.

B) Covariances of the Tapering Morphospace

The three axes of Figure 7 include 91.5% of all information, distributed as 25.6 on axis 1, 30.1 on axis 2, and 35.8 on axis 3. Table 4 presents the matrix of factor scores

for projections of variables upon these axes; we shall discuss the associations by decreasing information content of axes.

We recognize the third axis covariance from its similar expression in Table 3. The roughly equal projections for basic dimensions of the adult shell identify this axis as an expression of overall shell size (in Table 3, standardized whorl sizes covary with the raw measures of final size. Here they do not, reflecting the more common pattern of non-association between these two sets in *Cerion*).

Loadings of samples upon the third axis (Fig. 7) affirm this interpretation. This axis makes little distinction among islands, as each island harbors populations spanning a broad range of size. (Lability in size is characteristic of *Cerion*. All previous authors who sought biogeographic pattern with standard techniques of uni- and bivariate biometry were misled, by the large range of size *within* each region, to affirm a lack of distinctness between regions (see, for example, Hummelinck, 1940 and DeVries, 1974 on *C. uva*, corrected by Gould, 1984a. Multivariate techniques have revealed the basis in covariance sets for regional differences easily obscured by large variation in shell size). South Caicos samples, for example, span the entire range of third axis loadings. The generally larger shells of Grand Turk (45–100th percentile among all samples for length, and 51–86th for width) are distinguished by their higher loadings from the smaller shells of Providenciales (20–53rd percentile for length, 15–44th for width).

The second axis is crucial to our interpretation of the tapering morphotype, because it arrays each island in its own subfield, while ordering the Caicos islands in proper geographic sequence (see next subsection where we use this fact as the key for our taxonomic conclusion). Its covariances (Table 4) record a single and sensible pattern. Standardized whorl sizes are all prominent with heights for protoconch and fourth whorl (0.519 and 0.514) greater than widths (0.398 and 0.207). The only other strong values are for height/width ratio of the adult shell (a consequence of growing whorls higher than wide), and for ribs on the first whorl, a correlation that we have never before detected in *Cerion*. Note that this association records but one of the two major developmental pathways to slender shells—the other, and much more common, being simple addition of whorls (as discussed on p. 335). Samples from Providenciales load highest on this axis, South Caicos lowest. The percentile ranges of key variables fit this interpretation. Providenciales samples lie well above average in height/width ratio (64–84th percentile), but *below* in whorl number (27–34th percentile), indicating that relatively slender shells arise by growing high, not more, whorls.

The first axis records no major separation among islands. All high values are for South Caicos samples, but others from this island share lower values with populations from other islands. Turks Island samples are consistently low. The covariance ex-

TABLE 4. MATRIX OF FACTOR SCORES FOR THREE-AXIS SOLUTION OF ALL *C. REGINA* SAMPLES EXCLUDING THE SAND CAY DWARFS.

Measure	Axis 1	Axis 2	Axis 3
1. PROWID	−0.029	0.398	−0.053
2. FOURWID	0.005	0.207	0.173
3. NUMWHO	−0.002	0.046	0.244
4. RIBDENS	0.092	0.267	0.016
5. LENGTH	−0.071	0.093	0.334
6. WIDTH	−0.059	0.062	0.321
7. PROHT	−0.144	0.519	−0.056
8. FOURHT	−0.008	0.514	−0.140
9. FRSXHT	0.307	0.096	0.051
10. UMBWID	−0.070	0.021	0.372
11. LIPWID	0.069	0.044	0.162
12. LIPTHK	0.136	0.025	0.163
13. APHT	−0.053	0.013	0.328
14. APWID	−0.010	0.005	0.286
15. APROT	−0.023	0.043	0.341
16. EC	0.084	0.038	0.210
17. FA	0.391	0.188	−0.084
18. APTILT	−0.058	−0.016	0.249
19. WEIGHT	0.175	0.161	0.118
20. HWRATIO	0.352	0.237	−0.022
21. PRORAT	0.644	−0.156	−0.021
22. FOURRAT	0.321	−0.145	0.207

pressed in factor scores records a fundamental rule of *Cerion*'s growth, but one that we have not detected so clearly in our studies of northern Bahamian *Cerion*.

Consider the pattern in factor scores. Shells begin with low protoconch heights and average widths, yielding a relatively flat nucleus (width/height ratio of the protoconch scores maximally at 0.644). As the shell approaches middle growth, superficial expectations are subverted. Despite the initial advantage in width (still maintained at the fourth whorl, with width/height ratio scoring at 0.321), height asserts itself more and more prominently as the shell grows. Note the continual increase in scores for successive heights: −0.144 for the protoconch, −0.008 for the fourth whorl, and 0.307 for fourth-sixth whorl height. Thus, *early* widths are correlated with *later* heights (not later widths); or, in other words (and now interpreting), shells that begin quite flat compensate later by speeding up growth in height, and height compensation increases continually during middle growth.

We have noted this correlation of early widths with later heights again and again in our studies of land shells, not only in *Cerion* (Gould and Woodruff, 1978, 1986), but also in *Poecilozonites* (Gould, 1969b)—but its interpretation as compensation (keeping final dimensions within a limited range) had previously eluded us. We detect this pattern now because southern Bahamian *Cerion* should record it better. All *Cerion* with flat tops grow parallel-sided (or even width-*decreasing*) shells later in ontogeny, while shells that begin with a triangular top tend to maintain a gentle increase in width throughout growth. We have called the chief morphotype of the southern Bahamas "tapering" because most populations maintain a basic triangularity throughout growth. Yet the same tapering morphotype also includes the most initially flat-topped and later parallel-sided of all Bahamian *Cerion* (*C. malonei* on Long Island, populations of *C. columna* on Inagua, though the phenomenon reaches its extreme expression in species of the Cuban *C. dimidiatum* complex). This transition from triangular throughout growth to first flat-topped and then parallel-sided represents the range of expression for this first-axis covariance set. (We know, from a hybrid zone in Cuba, that direct transitions along this gradient occur, see Galler and Gould, 1979.) We had not detected this pattern in the northern Bahamas because the basic contrast between ribby and mottled morphotypes in this region expresses only a small segment of this range, while the full spate lies recorded among populations of the tapering morphotype.

We can now understand how this compensatory covariance orders populations of the Turks and Caicos. As with variation in size (third axis), all islands display a large range of loadings upon this axis, and few inter-island distinctions can be made. But Grand Turk samples are distinct in their high protoconchs (low width/height ratio from 2.04–2.33), while South Caicos populations tend to be flat-topped (range of 2.26–2.60, with only 1 sample of 20 below the maximal Grand Turk value of 2.33, and eight of 20 above 2.50). Yet this initial distinction is compensated in later growth as the early flatness of South Caicos shells engenders later exaggeration of height—for the final height/width ratios scarcely differ (range of 2.49–2.63 for Grand Turk and 2.44–2.78 for South Caicos).

C) A Taxonomic Decision: All Tapering Populations Belong to the Single Species, *Cerion regina*

The geographically localized and morphometrically restricted *C. blandi* and *C. lewisi* pose no taxonomic problems. They are distinct, immigrant forms and merit recognition as species (despite the hybridization of *C. blandi* with indigenous tapering populations, a pervasive phenomenon among *Cerion* taxa).

The problem of the Turks and Caicos *Cerion* fauna (both in the existing literature and in our morphometric data) centers upon widely varying populations of

the indigenous tapering morphotype. Can they all be gathered under one species, *C. regina* by priority (and a lovely name as "queen *Cerion*"), or have they differentiated to an extent meriting taxonomic subdivision? Three separate issues confront us: the status of morphometric outliers (the two dwarf samples), the validity of existing names in the literature, and the order and extent of morphometric variation among our measured samples.

We have already shown (see p. 336) that the dwarf samples, although morphometrically distant from the major clusters, are products of single transformations (and their correlated effects) noted again and again in dwarfed *Cerion* populations continuous with, and showing no sign of differentiation from, adjacent populations of normal size (Gould, 1984b; Gould and Woodruff, 1986; Woodruff and Gould, 1980).

Four species names exist in the literature for tapering forms from the Turks and Caicos. Clench (1961) had already synonymized the two Turks Island forms by sinking *C. incanoides* Pilsbry and Vanatta, 1895 into *C. regina* Pilsbry and Vanatta, 1895. We do not challenge this decision.

Do paratype populations of the remaining two species, *C. utowana abbotti* and *C. caicosense*, provide any evidence for valid distinction? *C. utowana abbotti* is easily dismissed by our morphometric evidence. As Figure 7 demonstrates, we include three samples named *C. utowana abbotti* by Clench (who described the taxon in 1961)—one from South Caicos (the paratypes), one from East Caicos and one from Long Cay on the Turks Bank. The South and East Caicos samples plot within the arrays of other samples from their island named *C. caicosense* by Clench. We have no other samples from Long Cay, but Clench's *C. utowana abbotti* lies within the morphospace of *C. caicosense*. We may therefore synonymize *C. utowana abbotti* into whatever status *C. caicosense* deserves.

The paratype sample of *C. caicosense* (Fig. 7) lies at the periphery of the South Caicos array (as formally designated taxa so often do), but clearly not apart from it. This population also has no claim for separation beyond its general membership in the South Caicos field.

We must, finally, consider the tapering morphospace itself (Fig. 7). The main argument for taxonomic distinction would lie in the separation of the South Caicos and Turks Island fields, for these are the type areas of the two available taxa, *C. regina* (Turks Island) and *C. caicosense* (South Caicos). Indeed, in the full morphospace of Figure 5, South Caicos lies as far from Grand Turk as the other legitimate taxa, *C. blandi* and *C. lewisi*, lie from each other.

The key to a proper taxonomy for the tapering morphotype lies in how samples from the other islands fit into the morphospace. If we find clear and separated clusters representing the geographically distinct Turks and Caicos banks, then we might admit the two existing names at some formal level. However, all representations of the morphospaces (Figs. 5–8) show the same pattern: populations from other islands of the Caicos Bank fully and continuously fill in the space between separated South Caicos and Turks Island clusters. We therefore find continuity in morphological distribution over the entire recorded range of the tapering morphotype, and no basis for taxonomic distinctions on this account.

But the pattern of intermediacy also speaks for unification through another aspect of its ordering. Our total array (Figs. 6 and 7) contains multiple samples from four islands of the Caicos Bank—Providenciales (3), Grand Caicos (3), East Caicos (4) and South Caicos (16). A comparison with the geography of islands (Fig. 1) shows that each island occupies a discrete part of the morphospace and, more importantly, that the four domains are arrayed in perfect geographical order from South Caicos through East and Grand to the most distant Providenciales (see Fig. 10). Moreover, the equally restricted mor-

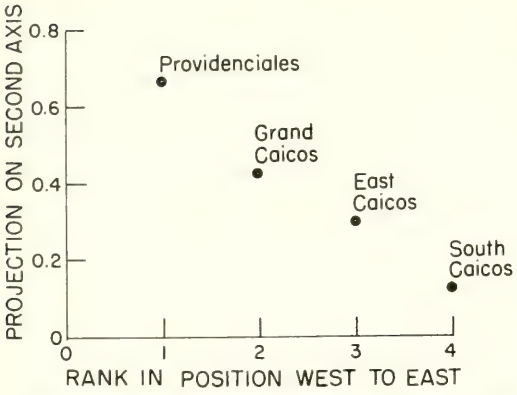

Figure 10. Plot of average projection of all samples upon the second axis versus rank in position along the north edge of the Caicos Bank, west to east.

phological domain of Grand Turk lies within this array.

We also know the basis in covariance for this clinal distribution (see last subsection): an increase in size of standardized early whorls towards Providenciales, with height increasing more than width, leading from the relatively flat-topped populations of South Caicos to the more slender and larger-whorled populations of Providenciales (see Fig. 3). This cline (Fig. 10) records standardized whorl sizes and their consequences for shape, not adult shell size; the Providenciales samples are, if anything, slightly smaller in size than most South Caicos populations, while each island forms a large and nondistinctive array for overall size (Grand Turk shells tend to be large, but one sample lies below the percentile means for adult length and height among tapering samples). All Caicos samples are therefore ordered by geography in a cline defined by a sensible determinant of shape and its associated covariances.

We used the same criterion of geographically ordered clinal distribution in morphology to unite a set of morphologically and geographically more distinct populations into the single species *C. striatellum* from Hispaniola to the Virgin Islands (Gould and Paull, 1977). For all these reasons, we find no basis for any taxonomic distinctions within the tapering morphotype of the Turks and Caicos islands. We therefore synonymize all previous taxa, and recognize only *C. regina* as the appropriate name for the indigenous *Cerion* of the Turks and Caicos islands. The *Cerion* fauna of this geographic outlier of the southern Bahamas therefore includes three species, the native *C. regina* from all major islands, and two restricted immigrants, *C. blandi* from Salt Cay, Turks Bank, and *C. lewisi* from several islands on the northwestern Caicos Bank. The indigenous species belongs to the common morphotype of its general region, while the two immigrants, both fortunately quite distinctive in morphology, have recognizable sources on nearby Cuba.

D) Genetics

This taxonomic conclusion, based solely on conchological and biogeographic data, is strongly supported by our population genetic survey. Although we cannot assess the genetic status of *C. blandi* and *C. lewisi*, we can document the strong genetic relatedness of *C. regina* from Providenciales and South Caicos on the Caicos Bank and Grand Turk on the Turks Bank.

Eight of the 16 genetically interpretable loci were monomorphic in the 17 samples studied: *Crp*, *Es-1*, *Es-6*, *Ldh-2*, *Mdh-2*, *Pgm-1*, *Pr-1*, *Sod-1*. The frequency of the various alleles at the seven polymorphic loci are shown in Tables 5–7. Three loci were diallelic (*Gapd*, *Gpi*, *Pgm-2*); *6Pgd* had three alleles, and three loci had up to four alleles segregating (*Es-2*, *Aat*, and *Mdh-1*). Data for acid and alkaline phosphatases are not reported as the results were uninterpretable. *Ldh-1* data are excluded as only three samples (758–760) were studied; they share a common allele, a second allele was segregating at 759–760, and a third allele was detected at 760.

Tables 5–7 show that the Grand Turk sample (766) is strikingly different from the others in its level of genetic variability. In contrast to the moderate levels of variation seen in all Caicos Bank samples the

TABLE 5. VARIATION IN ASPARTATE AMINOTRANSFERASE AND ESTERASE-2 ALLELE FREQUENCY.

Sample	$\bar{N}$*	$Aat^{1.2}$	$Aat^{1.0}$	$Aat^{0.7}$	$Aat^{0.4}$	$Es\text{-}2^{1.2}$	$Es\text{-}2^{1.1}$	$Es\text{-}2^{1.0}$	$Es\text{-}2^{0.9}$
					Providenciales				
770	29	0.05	0.95	—	—	—	—	1.00	—
772	31	0.00	1.00	—	—	—	0.03	0.97	—
					South Caicos				
753	32	0.03	0.97	—	—	—	—	1.00	—
757	29	0.10	0.90	—	—	—	—	1.00	—
754	32	0.03	0.97	—	—	—	—	1.00	—
758T	23	0.04	0.96	—	—	—	—	1.00	—
758	32	0.10	0.90	—	—	—	—	1.00	—
759	29	0.07	0.91	—	0.02	—	—	1.00	—
760	31	—	1.00	—	—	—	—	1.00	—
761	29	—	1.00	—	—	—	—	1.00	—
762	32	—	1.00	—	—	—	0.03	0.97	—
764	31	—	0.98	0.02	—	0.02	0.02	0.96	—
749	32	—	1.00	—	—	—	—	0.94	0.06
750	32	—	0.94	0.06	—	—	—	0.98	0.02
751	32	—	0.97	0.03	—	—	—	1.00	—
752	32	—	1.00	—	—	—	—	0.98	0.02
					Grand Turk				
766	31	—	1.00	—	—	—	—	1.00	—

* $\bar{N}$ = mean sample size per locus.

31 snails from Grand Turk were isogenic at all loci studied. However, as the Grand Turk sample is fixed for the common allele segregating at each polymorphic locus on South Caicos it is clearly closely related to the Caicos populations. We hypothesize that the Turks Island populations are descendants of a very few colonists from the Caicos Bank that, by chance, failed to carry or subsequently lost, the less frequent alleles of the source population. Such a scenario is in keeping with the traditional view that much interisland dispersal of *Cerion* results from the vagaries of hurricane transportation. At least one other species, *C. incanum*, is known to be isogenic in part of its range (Woodruff and Gould, 1987). In the lower Florida Keys four samples of 30 snails each were all monomorphic at 17 loci. One hundred km further north at Key Biscayne adjacent to the Florida mainland three samples showed variation at 1–2 loci.

The variation in allele frequencies reported in Tables 5–7 were used to establish the mating system and population structure of *C. regina*. The allele frequency estimates are reasonably robust as sample sizes were typically more than 30 individuals. A measure of the replicability of these estimates is provided by the comparison of data for samples 758T and 758; allele frequency differences at the three polymorphic loci (*Aat, Mdh-1, 6Pgd*) are insignificant. (Note also that both samples were treated morphologically and found indistinguishable, see Figs. 14, 16.)

We tested genotype frequency data for each variable locus in each sample for significant deviation from values expected under panmixia. In only three of 67 χ^2-tests did the probability that the frequencies were in Hardy-Weinberg equilibrium fall below 0.05. In these cases, however, the simple χ^2-tests were inappropriate and when exact probabilities were calculated these were all >0.15. We conclude that *C. regina*, an anatomical hermaphrodite, is outbreeding at random on Providenciales and South Caicos. This conclusion was supported by the calculation of Wright's index, F_{is}, the inbreeding coefficient of an

TABLE 6. VARIATION IN GLUCOSE PHOSPHATE ISOMERASE, GLYCERALDEHYDE DEHYDROGENASE AND MALATE DEHYDROGENASE-1 ALLELE FREQUENCY.

Sample	$Gpi^{1.4}$	$Gpi^{1.0}$	$Gapd^{1.0}$	$Gapd^{0.7}$	$Mdh\text{-}1^{1.2}$	$Mdh\text{-}1^{1.0}$	$Mdh\text{-}1^{0.8}$	$Mdh\text{-}1^{0.6}$
				Providenciales				
770	—	1.00	0.97	0.03	0.02	0.69	0.03	0.26
772	0.03	0.97	1.00	—	—	0.84	—	0.16
				South Caicos				
753	—	1.00	0.95	0.05	0.02	0.76	0.02	0.20
757	—	1.00	1.00	—	—	0.62	—	0.38
754	—	1.00	1.00	—	—	0.72	0.02	0.26
758T	—	1.00	1.00	—	—	0.50	—	0.50
758	—	1.00	1.00	—	—	0.47	0.03	0.50
759	0.02	0.98	1.00	—	0.04	0.60	0.04	0.32
760	0.02	0.98	1.00	—	—	0.58	—	0.42
761	—	1.00	1.00	—	—	0.68	0.02	0.30
762	0.02	0.98	1.00	—	—	0.91	—	0.09
764	0.02	0.98	1.00	—	—	0.94	—	0.06
749	—	1.00	0.92	0.08	—	0.83	0.14	0.03
750	0.03	0.97	0.86	0.14	—	0.92	—	0.08
751	0.02	0.98	0.94	0.06	—	0.88	—	0.12
752	0.02	0.98	0.86	0.14	—	0.72	—	0.28
				Grand Turk				
766	—	1.00	1.00	—	—	1.00	—	—

individual relative to its sample. The mean F_{is} for all seven polymorphic loci in all samples was 0.036 indicating that the snails sampled could all have been drawn from a single outbreeding metapopulation. Finally, we calculated coefficients of heterozygote deficiency for all variable loci and again found no significant heterozygote deficiency or excess in the samples. All three approaches indicate that *C. regina* is amphimictic on the Caicos Bank.

These tests cannot, of course, be applied to the monomorphic snails of Grand Turk (sample 766). It seems most unlikely that their isogenicity is due to a radical change in reproductive strategy—from outbreeding to self-fertilization—as the ability to do so is unknown in *Cerion*. Instead, as hypothesized herein, we attribute their genetics to a founder effect associated with the successful colonization of the Turks Bank by a few snails from the Caicos Bank. The study of additional samples from this, the most isolated of the Bahamian banks, should clarify this situation.

The remaining 16 samples representing 15 populations from Providenciales and South Caicos on the Caicos Bank are all moderately variable (Tables 5–7). The mean number of alleles per locus $\bar{A} = 1.3$ (range 1.2–1.5), the mean proportion of polymorphic loci $\bar{P} = 0.28$ (range 0.20–0.40), and the mean individual heterozygosity $\bar{H} = 0.06$ (range 0.05–0.09). The typical sample is thus polymorphic at four of the 15 loci and the most variable sample (750) at six loci. These levels of intrapopulation variability in *C. regina* are very similar to those determined for other well-characterized species of *Cerion* (Gould and Woodruff, 1978, 1986; Woodruff, 1975; Woodruff and Gould, 1987). Although these estimates of genetic variation are minimum estimates (as they are based on single-gel electrophoresis) they probably reflect 80% of the true variation at these structural gene loci (Ayala, 1983; Selander and Whittam, 1983).

The finding that *C. regina* is amphimictic permits us to use Nei's (1978) unbiased measures of multilocus genetic identity (I) and genetic distance (D) to

TABLE 7. VARIATION IN PHOSPHOGLUCOMUTASE-2 AND 6-PHOSPHOGLUCONATE DEHYDROGENASE ALLELE FREQUENCY AND IN OVERALL SAMPLE GENETIC VARIABILITY.

Sample	$Pgm\text{-}2^{1.3}$	$Pgm\text{-}2^{1.2}$	$6Pgd^{1.0}$	$6Pgd^{0.9}$	$6Pgd^{0.8}$	$\bar{A}$	P	$\bar{H}$
				Providenciales				
770	0.02	0.98	0.79	0.21	—	1.5	0.33	0.06
772	—	1.00	0.69	0.29	0.02	1.3	0.27	0.06
				South Caicos				
753	0.02	0.98	0.80	0.20	—	1.5	0.33	0.05
757	—	1.00	0.83	0.17	—	1.2	0.20	0.06
754	—	1.00	0.76	0.24	—	1.3	0.20	0.05
758T	—	1.00	0.68	0.32	—	1.2	0.20	0.06
758	—	1.00	0.59	0.41	—	1.3	0.20	0.09
759	0.02	0.98	0.64	0.36	—	1.5	0.33	0.08
760	0.02	0.98	0.71	0.29	—	1.3	0.27	0.07
761	0.02	0.98	0.76	0.24	—	1.3	0.20	0.05
762	—	1.00	0.56	0.39	0.05	1.3	0.27	0.05
764	—	1.00	0.55	0.43	0.02	1.5	0.33	0.05
749	—	1.00	0.84	0.16	—	1.3	0.27	0.05
750	—	1.00	0.69	0.31	—	1.4	0.40	0.06
751	—	1.00	0.66	0.34	—	1.3	0.33	0.06
752	—	1.00	0.60	0.40	—	1.3	0.33	0.08
				Grand Turk				
766	—	1.00	1.00	—	—	1.0	0.0	0.0

$\bar{A}$ = mean no. alleles per locus, P = proportion of loci polymorphic, $\bar{H}$ = mean individual heterozygosity per locus.

assess the overall pattern of differentiation within this species. The results show that only minor geographic differentiation has occurred, a finding concordant with the calculation of Wright's fixation index (F_{st} = 0.08). A similarity matrix (available from D.S.W.) for all pairwise comparisons of the 17 samples showed I values to range from 1.00 to 0.982 on South Caicos. Overall similarity is higher than this range suggests as 75% of the 136 values ≥0.995. The lowest I value (0.971) involved samples 758 (northeast South Caicos) and 766 (Grand Turk).

The similarity matrix can be visualized by cluster analysis. Here we present a genetic distance phenogram (where $D = -\ln I$) prepared by the unweighted pair group with averaging (UPGMA) algorithm (Fig. 11). Nei's genetic distance, D, a multilocus measure of intersample differences, may range between 0.00 (identity) and infinity. Within a group of sexually reproducing organisms D values increase with taxonomic distance. For example, only about 2% of 7,000 estimates of D between conspecific populations of a wide range of organisms exceed 0.10 and only 2% of 900 estimates of D between congeneric species fell below 0.15. Interspecific genetic distances of mammals, fish, and reptiles are typically in the range of D = 0.3–0.5 (Avise and Aquadro, 1982) and published results for mollusks are also generally in this range (Woodruff and Merenlender, in prep.). *Cerion* (and birds) are a little exceptional in that they show less differentiation within and between species than most other groups. Nevertheless, no *Cerion* species or semispecies are known where the interspecific D is less than 0.05 or the intraspecific D exceeds a similar value (Gould and Woodruff, 1986; Woodruff and Gould, 1980, 1987).

Given this background it is clear from Figure 11 that *C. regina* is remarkably homogenous genetically. After pairwise averaging, the greatest D value separating clusters of samples is only 0.01. It must be remembered that the error on such small

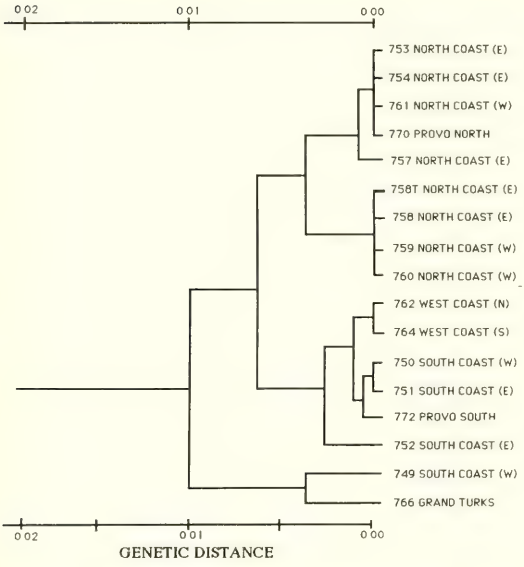

Figure 11. A dendrogram based on UPGMA clustering of 17 samples of *Cerion regina* from Providenciales, South Caicos and Grand Turk using the unbiased genetic distance (*D*) of Nei (1978). Samples are identified according to their locality number and geographic location (*PROVO* = Providenciales; *N*orth, *S*outh, *E*ast, *W*est).

branch-point estimates exceeds the *D* value itself; no great biological significance can be placed on the subclustering in Figure 11. Notwithstanding this caution, we immediately note two interesting aspects of clustering in the 17 samples. The first is that the Providenciales samples are embedded in the South Caicos cluster. Samples 770 and 772 from the north (bank-edge) and south (bank-interior) coasts of Providenciales are genetically indistinguishable from samples from South Caicos. Most interestingly, these two samples cluster with the biogeographically equivalent groups on South Caicos, i.e., 770 with the northeastern bank-edge group, 772 with the southwestern bank-interior group. (This within island patterning will be discussed in more detail in section VII.) The second significant result in Figure 11 involves Grand Turk (766): *Cerion* on this isolated island bank are indistinguishable from those of the Caicos Bank. The only distinction (manifest as $\bar{D} = 0.01$) stems directly from the fact that Grand Turk's snails are fixed for the common alleles on the Caicos Bank. There is thus no genetic evidence to support the recognition of *C. caicosense* as a separate species. Again, no special significance can be placed on specific branch-points at this level of differentiation so the clustering of sample 766 with sample 749 (southwest South Caicos) does not indicate that the Turks Bank populations were founded by this Caicos population. In fact, individual snails homozygous at all variable loci for the same alleles that are fixed on Grand Turk occur in every one of the South Caicos and Providenciales samples.

The genetic data therefore lead to the following conclusions. *C. regina* is a typical amphimictic species. Despite fragmentation of populations today on two island banks separated by the 32 km wide Turks Island Passage there is no evidence of genetic differentiation. Similarly, the populations on Providenciales and South Caicos, presumably continuous a few thousand years ago but separated today by about 100 km of water, are genetically indistinguishable. Such low levels of genetic differentiation are typical of other known species of *Cerion* and of conspecific populations generally.

E) A Note on Minor Axes and General Geometry

We have seen that the major axes of our factor analyses sort the islands into discrete groups and order them into a clinal array that supports the unification of all populations into the single species *Cerion regina*.

We have argued in previous works (Gould and Woodruff, 1978, 1986 in particular) that minor axes should not be ignored, for they may display significant biological information based on few variables in few samples (even if statistically "insignificant" in another, technical sense of the word). In the *C. regina* morphospace, most minor axes yield no general interpretation, for they capture only the peculiarities of

single samples for single measures. But the fourth axis, carrying some 10% of information, displays a coherent and interesting aspect of covariance well known from all our *Cerion* studies. Note, in Table 8, that three of the highest scores form a well-known covariance set based on whorl number and its consequences for shape—many whorls (0.390) produce a high (0.225), not a wide (0.012), shell because later whorls, in the second allometric phase, add height but little or no width, leading to large height/width ratio of the adult shell (0.416).

If we now consider the two highest negative scores, we note standardized whorl sizes of the early shell—fourth whorl width at −0.277 and fourth to sixth whorl height at −0.248. This negative association is the pervasive constraint—we call it the constraint covariance—that we have identified in all *Cerion* studies (see particularly Gould and Paull, 1977; Gould and Woodruff, 1978). If a shell begins by growing larger than average whorls, it will necessarily grow fewer of them to reach the same final size. Thus, when final sizes fall in a limited range, we find negative associations between whorl numbers and measures of standardized whorl sizes. This constraint holds particular interest because it imposes forced correlations for basic shape as well. The shell with small and many whorls will be slender and parallel-sided, while the alternative with fewer, larger whorls will be squatter and continually increasing in width. These forced correlations arise because shells, in the second allometric phase, add height but little or no width. The more whorls added in this phase, the more slender the adult shell (Gould, 1984b).

When we plot (Fig. 12) all samples onto this constraint axis, we note a different pattern. High values do not mark any geographic location, but rather pluck out a sample or two from each major place; the five highest loadings include two for East Caicos and one each for Grand Caicos, Providenciales and Grand Turk. (Two East Caicos samples are high, but the other two from this island are lower than average.) The constraint covariance is a pervasive rule of growth within all *Cerion*, not the unique association of a single place. Thus, it can "attract" samples from any region that happen to grow (in this case) with small whorls, and thereby develop with the forced correlations so implied. Finally, we note in Figure 13 that the constraint covariance acts in the same way upon the full morphospace, selecting one or two samples from all taxa and regions by virtue of smaller than average whorls that can occur in *any* taxon or region, and then carry their train of enjoined consequences with them.

TABLE 8. FACTOR SCORES ON FOURTH AXIS (12.6% OF INFORMATION) OF AN ANALYSIS FOR ALL TAPERING SAMPLES EXCEPT FOR SAND CAY DWARFS.

Measure	Axis 4
1. PROWID	−0.210
2. FOURWID	−0.277
3. NUMWHO	0.390
4. RIBDENS	0.442
5. LENGTH	0.225
6. WIDTH	0.012
7. PROHT	0.164
8. FOURHT	−0.097
9. FRSXHT	−0.248
10. UMBWID	0.204
11. LIPWID	0.138
12. LIPTHK	0.030
13. APHT	0.132
14. APWID	0.099
15. APROT	0.272
16. EC	−0.000
17. FA	−0.108
18. APTILT	0.243
19. WEIGHT	−0.084
20. HWRATIO	0.416
21. PRORAT	−0.115
22. FOURRAT	−0.031

VII. Covariation at Level Three: Does Order Still Reign Within Islands?

Descending now to the finest level of among-sample relationships, we shall consider the distribution of samples for a single island, our most completely collected

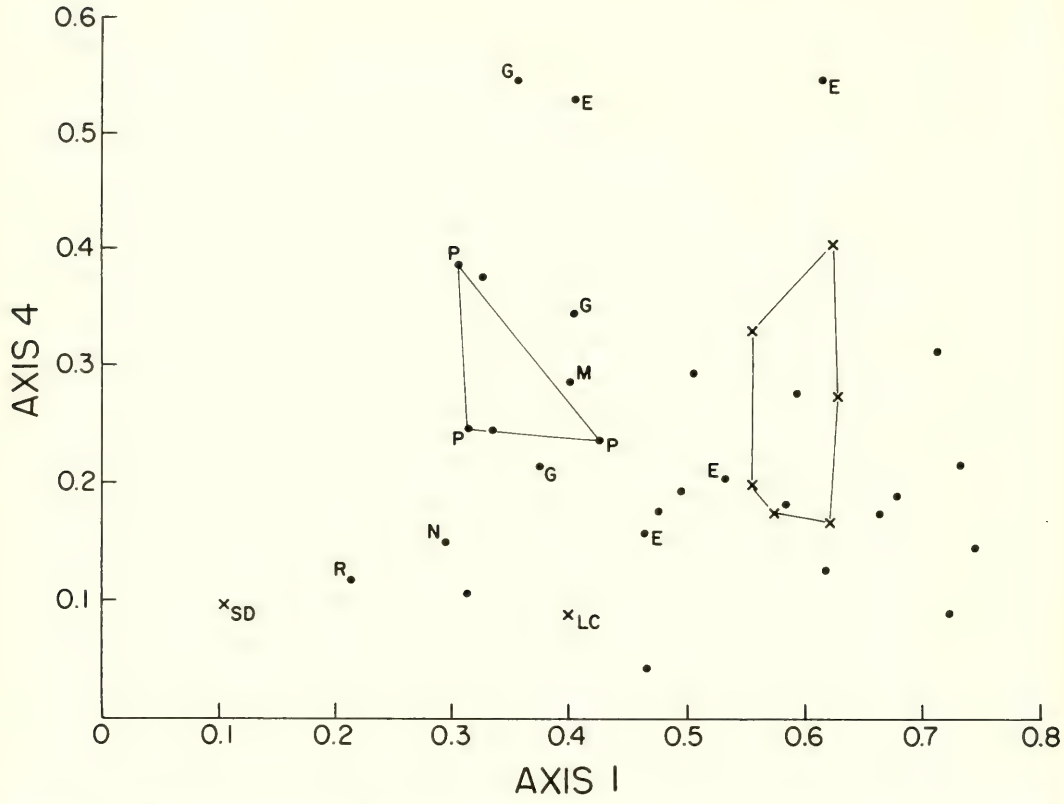

Figure 12. Loadings of mean vectors for *C. regina* samples upon first and fourth axes. Symbols as in Figure 5 except Caicos Bank samples are dots and Turks Bank samples are crosses. Note that the fourth axis, expressing the geometrically necessary negative covariation of whorl size and whorl number, does not identify any particular region, but isolates a few samples from several regions.

South Caicos, within their own morphospace. We have shown (both here and in all our *Cerion* studies of other island groups) that geographic variation *within* islands also displays ordered pattern rather than random arrays. (Thus, older claims for crazy-quilt distributions are false at all levels—from the highest of taxonomic separation between major banks to the finest of minor differentiation within single taxa on single islands.) We have found repeated order based on recurrent habitat (Gould, 1984a on windswept platforms versus secluded valleys, and on limestone or volcanic substrates in *C. uva*), and on simple geographic contiguity [distinction of Treasure Cay samples of *C. bendalli* on Abaco (Gould and Woodruff, 1978); or of offlying cay populations of *C. glans* on New Providence (Gould and Woodruff, 1986)]. We now report a similar coherence for tapering samples on South Caicos as well.

The five-axis solution for South Caicos samples seems to capture all important dimensions of covariance, with no subsequent axis including even one percent of information. We plot, as Figure 14, the loadings of all South Caicos samples (excluding the subfossil dwarf outlier, 765, discussed earlier) upon the two axes explaining most information (axis 1 at 37.9% and 3 at 23.9%; no other axis exceeds 15%). A comparison of these loadings with geo-

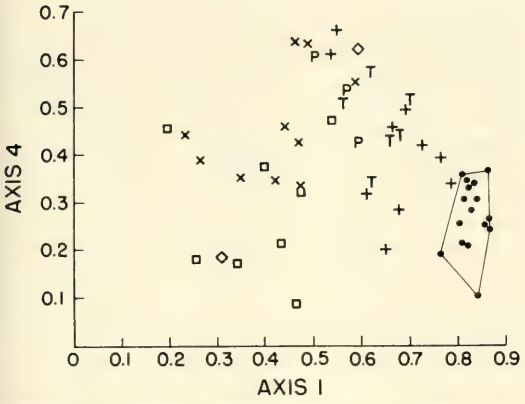

Figure 13. Loadings of mean vectors for all samples upon first and fourth axes. Note, as in Figure 12, that the fourth axis isolates some samples from all regions and taxa. As in Figure 5, crosses are *C. blandi* and squares are *C. lewisi*. For *C. regina* dots are South Caicos; plusses are other Caicos islands; T are Grand Turk; and diamonds are other Turks Bank samples.

graphic position (Fig. 15) shows that samples plot into the South Caicos morphospace largely by geographic location; subregions of this small island can be iden-

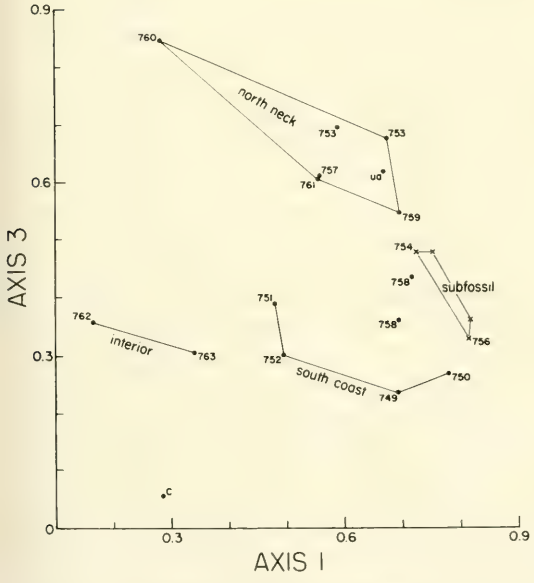

Figure 14. Loadings for South Caicos samples only. Dots are modern samples, crosses are fossils. All points include our collection number (see Fig. 14) except for the two paratype samples collected previously: c is *C. caicosense*; ua is *C. utowana abbotti*. Note good separation by region and time, even on this very small island.

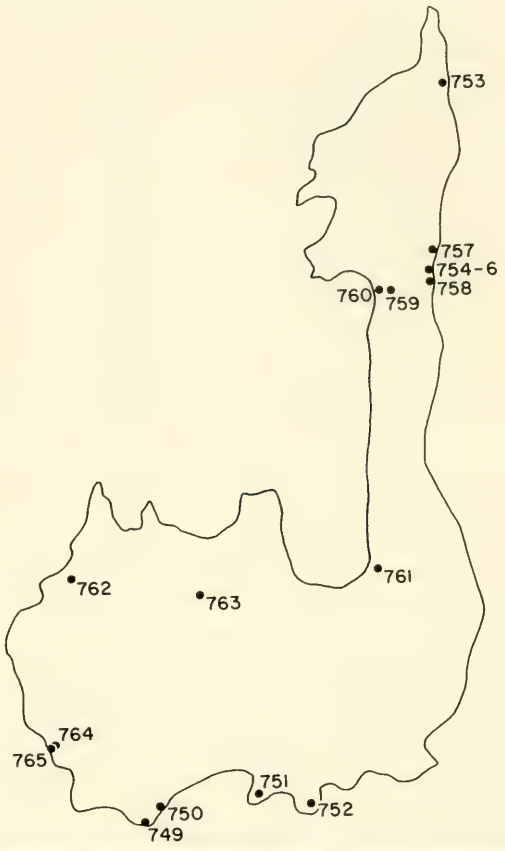

Figure 15. Outline map of South Caicos showing location of our samples.

tified by morphology. In addition, we gain some confidence in our methods of measurement by noting that for two locations with two samples each (753 and 758), the two loadings for each place are adjacent. (In each location, snails in one sample came from a single tree, and the other sample from surrounding grass and bushes.)

The first axis distinguishes subfossil samples by high loadings and the two interior samples (at the airstrip) by low loadings. The third axis contrasts samples from the northern neck of the island (high loadings) with central and southern samples. Taken together, we may identify four broad temporal and geographic domains (not distinct clusters since they overlap, but not random arrays because they do not interpenetrate):

TABLE 9. SCORES OF FIVE-AXIS SOLUTION FOR SOUTH CAICOS SAMPLES.

Measure	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
1. PROWID	0.331	−0.043	−0.011	0.061	0.156
2. FOURWID	0.260	0.025	0.142	0.155	0.320
3. NUMWHO	0.079	−0.031	0.170	−0.365	−0.133
4. LENGTH	0.226	−0.070	0.096	−0.091	−0.038
5. WIDTH	0.206	−0.114	0.171	−0.031	0.156
6. PROHT	0.380	−0.076	−0.209	−0.286	−0.016
7. FOURHT	0.403	0.473	−0.124	0.306	−0.015
8. FRSXHT	0.341	0.024	0.052	0.233	0.170
9. UMBWID	0.030	0.053	0.427	0.052	−0.047
10. LIPWID	0.240	0.063	0.092	0.078	−0.292
11. LIPTHK	0.167	−0.030	0.066	−0.066	−0.113
12. APHT	0.230	−0.082	0.146	−0.008	−0.044
13. APWID	0.188	−0.096	0.178	−0.046	0.040
14. APROT	0.192	−0.019	0.312	−0.072	−0.214
15. EC	0.122	−0.145	0.014	−0.371	0.229
16. FA	0.056	0.346	−0.255	−0.475	0.391
17. APTILT	−0.108	0.005	0.486	−0.129	−0.126
18. HWRATIO	0.076	0.409	−0.031	−0.397	−0.448
19. PRORAT	−0.209	0.638	0.330	0.066	0.235
20. FOURRAT	−0.094	−0.103	0.308	−0.196	0.416

subfossils (all from the northern neck), modern samples from the northern neck, the south coast, and the western interior at the airstrip. We were surprised (and pleased) to find these distinctions on such a small island with populations in broad contact. The type sample of *C. caicosense*, with high loadings on the second axis (see below), plots with low loadings on both axes of Figure 14.

The patterns of covariance revealed by factor scores help to explain these patterns among samples (Table 9). We recognize, in the nearly uniform scores for all measures of size (final and whorl-standardized in this case) on the first axis (37.9%), the signature of general size that we have identified at all levels in this study. We can therefore identify the basis for distinction of the large subfossils. More important, we now note for the first time in the tapering morphotype the same basic pattern that sets relationships of size in the ribby and mottled morphotypes of the northern Bahamas: large and thick shells of exposed coasts contrasting with smaller and thinner shells of calm coasts and island interiors. Note this contrast for divisions *within* both the southern and northern domains on South Caicos. In the north, the samples of the exposed, bank-edge east coast (753, 758) load high, and the calm, bank-interior west coast low (760). In the south, coastal samples are high (749–752), interior samples low (762–763).

The second axis (14.4% of information), with high loadings only for the *C. caicosense* paratypes and two southern samples (752, 762) expresses an aspect of the central covariance regulating *Cerion*'s shape, and discussed above (p. 337): the play-off between initial flatness and later acceleration in height (leading to an apparent contrast that actually represents two expressions of the same rule at opposite extremes of its action—a shell roughly triangular throughout and continually expanding in width, versus a flat-topped shell compensated later by rapid growth in height to produce a parallel-sided adult shell). *C. caicosense* is, apparently, not a valid taxon, but the name given to one end of this continuity in a key morphogenetic rule—the flattened nucleus and later compensation in height most characteristic of South Caicos' unique samples (see Figs. 5–

8). All high scores on the second axis fit this interpretation [initial flatness (width/height ratio of the protoconch at 0.638), followed by compensatory height (fourth whorl height at 0.473, and last whorl height FA at 0.346), leading to a high-spired shell (final height/width ratio at 0.409)].

The third axis (23.9%), the other major basis of sensible distinctions among South Caicos samples, captures another aspect of this key covariance in shape. Initial flatness, this time of both protoconch (measure 19 at 0.330) and fourth whorl (measure 20 at 0.308), is compensated by continually increasing assertion of standardized height (smooth increase of scores for measures 6–8 from −0.209 to −0.124 to 0.052). In addition (and if related by developmental architecture, we do not know how), we find correlated high scores for the three measures of accentuated change of shape in the adult aperture, the third allometric phase of *Cerion* (apertural rotation, measure 14, at 0.312; apertural tilt, measure 17, at 0.486; and umbilical width, measure 10, increasing as the aperture tilts away, at 0.427). Thus, samples with high loadings on this axis have strong apertures and flattened tops, followed by later compensatory growth in height. This distinction sets the primary contrast between northern and southern samples on South Caicos.

The fourth and fifth axes (14.7 and 6.6% of information) do not make broad geographic distinctions among samples. Both emphasize the standardized sizes of early whorls in their covariances, and we find, as we have before (see Gould and Paull, 1977, for example), a contrast between heights (fourth axis) and widths (fifth axis). Other high scores associate sensibly with these standardized sizes according to the principal constraint that we have identified in *Cerion* (discussed in section VI E): under limitations upon final shell size, large early whorls imply fewer total whorls, leading to forced correlations in final shape, especially the building of greater height along the many and small whorled pathways. Note the negative association of whorl number (−0.365) and final height/width ratio (−0.397) with high scores for standardized heights (0.306 for fourth whorl, 0.233 for fourth to sixth whorl) on axis 4. The same pattern repeats on the fifth axis, where strong standardized widths (0.156 for the protoconch, 0.320 for the fourth whorl) associate negatively with whorl number (−0.133), final height/width ratio (−0.448), and also yield in this case, a flattened top produced by the strong early widths (unmatched by heights): 0.235 for width/height of protoconch, and 0.416 for width/height at the fourth whorl.

The triangular, three axis solution collapses this covariance by amalgamating general size with one aspect of the key shape covariance (the flat-top later-height principle) on the first axis (now 55.8% of information), according (as in the 5-axis solution) another aspect of this key shape covariance to the second axis (now 19.2%), and joining the fourth and fifth axes into a single axis (the third at 17.5%) by incorporating both standardized heights and widths, and recording the chief constraint of negative interaction between large early sizes and few total whorls. These covariances are expressed in Table 10. This arrangement divides the determinants of form within the South Caicos morphospace into its three major principles—size on the first axis, the major covariance determining variation in shape on the second (the compensation of initial flatness by later growth in height), and the major constraint forcing correlations among characters on the third (negative association between whorl size and whorl number under limitations upon the range of final shell size).

The triangular plot of sample loadings (Fig. 16) makes the same distinctions as Figure 14, with tighter clustering around the now more dominant first axis, and greater separation of the *C. caicosense* paratypes on the second axis, and the interior samples (762–763) on the third. This figure also records an important point about

TABLE 10. SCORES OF THREE-AXIS SOLUTION FOR SOUTH CAICOS SAMPLES.

Measure	Axis 1	Axis 2	Axis 3
1. PROWID	0.302	0.097	0.172
2. FOURWID	0.363	0.124	0.183
3. NUMWHO	0.127	−0.061	−0.375
4. LENGTH	0.230	−0.029	−0.063
5. WIDTH	0.315	−0.048	0.005
6. PROHT	0.197	0.129	−0.029
7. FOURHT	0.166	0.527	0.260
8. FRSXHT	0.333	0.126	0.265
9. UMBWID	0.230	−0.098	−0.183
10. LIPWID	0.143	0.007	−0.025
11. LIPTHK	0.140	−0.025	−0.070
12. APHT	0.258	−0.062	−0.019
13. APWID	0.269	−0.071	−0.048
14. APROT	0.261	−0.113	−0.215
15. EC	0.197	0.001	−0.174
16. FA	−0.025	0.543	−0.218
17. APTILT	0.142	−0.202	−0.389
18. HWRATIO	−0.139	0.296	−0.493
19. PRORAT	−0.017	0.444	−0.245
20. FOURRAT	0.229	−0.081	−0.186

taxonomic practice. We see that the invalid names *C. utowana abbotti* and *C. caicosense* are not geographically defined areas of microdifferentiation, but extreme expressions (within the morphospace) of tendencies in covariance common to the entire sample—*C. utowana abbotti* by size, *C. caicosense* by the major shape covariance set.

Thus, variation within South Caicos is both geographically coherent and expressed along the major lines of developmental channeling in *Cerion*—a fine example of the interplay (not antithesis) between themes of constraint and adaptation.

A similar pattern of geographic coherence can be seen in the genetic data for the 13 populations sampled on this small island. Figure 11 clearly shows two clusters of samples: those from the northeast of the island and those from the south and west coasts. (Note that the populations sampled are the same as those discussed morphometrically except for the omission of 763 and the addition of the west coast 764.) Inspection of Tables 5–7 reveals the minor differentiation underlying this dichotomy. The northern end of the island is characterized by higher frequencies of $Aat^{1.2}$, $Mdh\text{-}1^{1.2}$, $Mdh\text{-}1^{0.8}$, $Mdh\text{-}1^{0.6}$ and $Pgm\text{-}2^{1.3}$. The southern and western populations have higher frequencies of $Aat^{0.7}$, $Es\text{-}2^{1.2}$, $Es\text{-}2^{1.1}$, $Es\text{-}2^{0.9}$, $Gpi^{1.4}$, $Gapd^{0.7}$ and $6Pgd^{0.8}$. The allele $6Pgd^{1.0}$ shows apparently clinal variation: decreasing in frequency from 0.8 in the north to about 0.55 in the southwest, with the south coast samples showing intermediate values. The overall pattern of geographic differentiation on South Caicos thus involves all seven polymorphic loci and is remarkably similar to the pattern revealed morphometrically.

Certain parallels can be drawn between the geographic pattern of genetic differentiation seen on South Caicos and that found previously in the northern Bahamas. On New Providence Island, for example, we found two imperfectly isolated species with an interspecific D of about 0.05 (Gould and Woodruff, 1986). The two taxa showed consistent differences in shell morphology and distribution. *C. glans*, typically with unmottled strongly ribbed shells, is restricted to coastal sites within 3–7 km of the edge of the island bank. *C. gubernatorium*, on the other hand, has mottled finely ribbed shells and is found in the interior of the island and on coasts adjacent to the bank interior. It has not been found at the bank edge. Today the two species hybridize and morphological hybrids have been collected over distances of <1 km where the ranges come into contact. Genetic introgression is, however, more extensive: *C. gubernatorium* alleles have swept into the bank-edge coast populations of *C. glans* and *C. glans* alleles have introgressed 3 km beyond the limits of morphological hybridity. Today, we find genetically "pure" *C. gubernatorium* restricted to the southeast corner of this narrow island (average width 7 km) where they are 5–7 km away from the influence of *C. glans*. The genetic hybrid zone on New Providence is an area of genetic anomaly. Hybrid populations may show

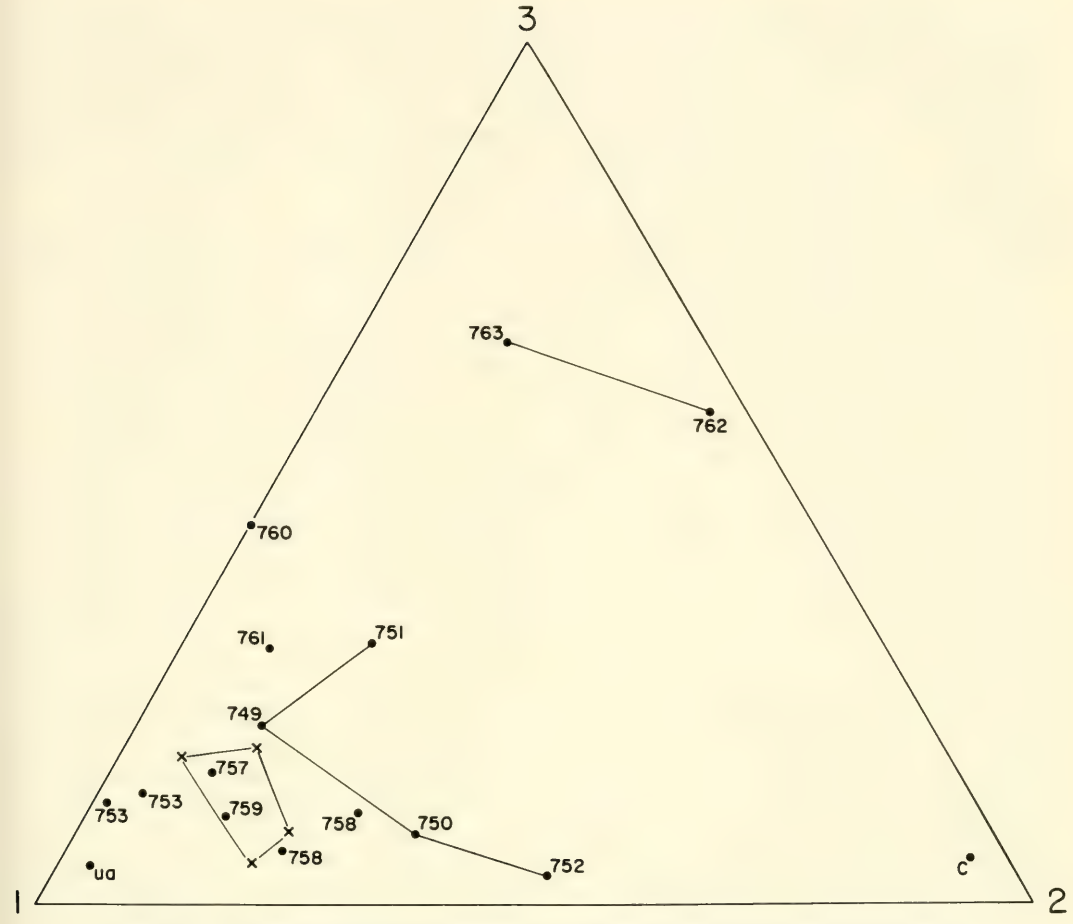

Figure 16. Loadings for South Caicos samples on first three varimax axes. Symbols as on Figure 14.

slightly elevated levels of genetic variability (*P*, *H*) and are frequently characterized by the segregation of rare or unique alleles at frequencies far higher than those seen in homospecific populations (Woodruff, 1981). In addition, several step clines in allele frequencies are associated with the hybrid zone. The pattern of clinal variation (bank-edge to bank-interior coasts) of several alleles on New Providence (*6Pgd*$^{1.0}$, *Es-2*$^{1.09}$, *Pgm-2*$^{1.2}$) is, in fact, quite similar to that seen on South Caicos and Providenciales. The obvious question arising from the similarities of New Providence and South Caicos is whether today's South Caicos populations represent the legacy of a historical interaction between two species? Has the evidence for a former bank-interior species all but disappeared on this smaller island?

If the Caicos Bank had been originally occupied by a bank-edge and a bank-interior species comparable to those seen on the Great Bahama Bank and the Little Bahama Bank islands, we would make two predictions about the situation on South Caicos based on our earlier work. First, the island is too small for genetically "pure" populations of the interior taxon to endure. All living populations are found within 7 km of the bank-edge and will therefore be introgressed to varying degrees. Present

island size limits our ability to examine this prediction. Nevertheless, additional collecting on bank-interior coasts of North Caicos, Grand Caicos and East Caicos might illuminate this issue as such populations live >10 km from the modern bank-edge coasts. Second, we would predict that the populations furthest from the bank-edge coasts will show more evidence for hybridity than those at the coast. Such interior populations as 764 and 762 might show elevated levels of *P* or *H*, increased heterozygote deficiency or excess, or higher frequencies of rare or unique alleles. There is, however, no evidence for consistent geographic trends in *P*, *H*, or departure from random mating. Only in the case of the rare allele phenomenon are the interior populations at all unusual. Unexpected alleles were, in fact, detected in samples 764 and 762 at $Aat^{0.7}$, $Es\text{-}2^{1.1}$, $Es\text{-}2^{1.2}$, and $6Pgd^{0.8}$ at frequencies of 0.02–0.05. Additional rare alleles occurred at 759–761, sites which are also geographically intermediate between the bank-edge and the bank-interior coasts: $Pgm\text{-}2^{1.3}$, $Mdh\text{-}1^{1.2}$, $Aat^{0.4}$. Two of these rare alleles ($6Pgd^{0.8}$ and $Es\text{-}2^{1.1}$) were also detected on Providenciales in sample 772 from the southern bank-interior coast. These rare alleles may be a legacy of a former hybrid zone—that is, they may constitute the genetic anomaly seen in other *Cerion* hybrid zones. Alternatively, these currently rare alleles may once have occurred at higher frequencies in the conspecific bank-interior populations of *C. regina* that until a few thousand years ago occupied an area 20 times as extensive as today's islands.

These hints of genetic vestiges for another taxon within *C. regina* are intriguing (see final section), but do not alter our conclusion that all indigenous *Cerion* so far collected in the Turks and Caicos (excluding the recent immigrants *C. blandi* and *C. lewisi*) belong to the single species *C. regina*. Interspecific hybridization is so rampant in *Cerion* (Woodruff and Gould, 1987) that most widespread species of *Cerion* probably maintain, at least in parts of their range, introgressed genetic material of other taxa. When these introgressed contributions are minor and, especially (as here) when they are associated with no morphological expression of intermediacy, we must retain the name of the dominant component.

We faced the same problem in determining the proper name of the mottled morphotype on New Providence Island (Gould and Woodruff, 1986). *C. gubernatorium*, the oldest name, was originally given to populations that contain "phantom" genes of *C. agassizi*, a prominent fossil taxon now extinct on New Providence, but still living on the adjacent islands of Cat and Eleuthera (and also hybridizing with mottled *Cerion* in both places). Despite these genetic "phantoms," and some morphological remnant of *C. agassizi* as well, we accepted *C. gubernatorium* as the correct name for all mottled *Cerion* of New Providence because the *C. agassizi* signature in these populations is so small relative to the morphological and genetic expression of ordinary (and abundant) mottled *Cerion*. The evidence for phantoms of another taxon within some samples of *C. regina* is far weaker, and shall not alter our taxonomic conclusion that all known Turks and Caicos samples of the tapering morphotype belong to the single species, *C. regina*. We must, however, bear in mind what is no longer only the intriguing possibility, but by now the established fact that important features of geographic variability within many *Cerion* taxa are the product of introgression, not simple local adaptation.

VIII. Level Four: Covariation Within Samples

Variation in average form among samples (treated in all previous sections), and differences among organisms within a population, are so fundamentally distinct in concept that we anticipate no necessary relationship between their patterns. Yet all *Cerion* species grow with the same allometries (despite enormous differences in

TABLE 11. SCORES FOR FIVE-AXIS SOLUTION OF SPECIMENS WITHIN SAMPLE 753.

Measure	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
1. PROWID	0.242	0.020	0.240	0.125	−0.130
2. FOURWID	0.387	0.166	0.075	0.094	−0.025
3. NUMWHO	−0.216	−0.402	0.133	0.027	0.024
4. RIBDENS	−0.064	−0.084	0.358	0.206	0.071
5. LENGTH	0.065	−0.314	0.075	−0.158	0.054
6. WIDTH	0.308	−0.109	−0.009	−0.220	0.180
7. PROHT	−0.117	−0.052	0.539	−0.144	0.204
8. FOURHT	0.205	0.168	0.408	0.106	−0.116
9. FRSXHT	0.365	0.178	0.179	0.113	−0.051
10. UMBWID	0.013	0.126	0.320	0.184	0.367
11. LIPWID	0.258	−0.089	−0.061	0.101	0.143
12. LIPTHK	0.019	−0.239	0.029	0.185	−0.045
13. APHT	0.287	−0.094	−0.085	−0.233	0.443
14. APWID	0.254	−0.147	−0.181	−0.033	0.317
15. APROT	−0.065	−0.041	−0.058	0.476	0.294
16. EC	0.075	−0.407	−0.088	0.245	−0.245
17. FA	0.259	−0.295	0.194	−0.205	−0.352
18. APTILT	−0.131	−0.024	−0.030	0.435	0.191
19. WEIGHT	0.049	−0.292	0.092	−0.129	0.175
20. HWRATIO	−0.140	−0.344	0.190	0.063	−0.079
21. PRORAT	0.304	−0.042	−0.119	0.342	−0.264
22. FOURRAT	0.175	−0.243	−0.203	0.158	0.130

outcome), and the gastropod shell, in general, is a highly constrained structure replete with geometrically forced covariances. Thus, we expect that similar patterns might regulate the different styles of within- and among-sample variation (see Gould and Paull, 1977; Gould and Woodruff, 1978 for correspondences in other *Cerion* species). Sample means might represent different states along tracks of covariance common to the within-sample variation of all populations.

Since all shells are adults and their range in size is not large, our samples of 20 do not provide enough specimens for stable covariance structures within populations (though they define mean values adequately). But we measured a larger number of shells (as a split sample to test for proximity in morphospace) for South Caicos *C. regina* at locality 753 (35 individuals). Table 11 presents factor scores for this enlarged sample. The structure of covariation is stable at five meaningful axes (93.2% of information). (In a sequence of reduction from 10 axes down, none of the first five axes ever dip below 7%, and no subsequent axis reaches 2% of total information.)

The first axis unites the two major patterns of constrained covariance that we have discussed throughout this paper. First, we see all chief components of the compensatory (flat top with later height) covariance that sets the primary pathway of variation in shape from obtusely triangular in cross section throughout, to distinctly flat topped at first, and parallel-sided during later growth. Note high scores for the two ratio measures of flat top (width/height of protoconch at 0.304, and of the fourth whorl at 0.175). Protoconch width (0.242) greatly exceeds protoconch height (negative at −0.117), but height is beginning to catch up by the fourth whorl (0.387 for width, 0.205 for height). The three scores for successive heights increase continually to record the compensation (−0.117 to 0.205 to 0.365).

Second, we note all elements of the major constraint imposed by geometric necessity: large whorls imply fewer adult

whorls under conditions of restricted range in adult size. Intermediate standardized whorl sizes score highly (fourth width and height at 0.387 and 0.205, and fourth to sixth height at 0.365). These large whorls imply fewer total whorls (−0.216), with the usual consequence of squatter adult shells, since later whorls add relatively more height than width (height/width ratio of adult shell at −0.140).

The second axis primarily records whorl number (−0.402) and its consequences in shape for a high, but not wide, shell (−0.314 for height, −0.109 for width, since later whorls add relatively more height than width), and final shape (height/width ratio at −0.344). This primary association also brings along, as on axis 1, the forced negative covariances with standardized whorl sizes (0.166 for fourth width, 0.168 for fourth height, 0.178 for fourth to sixth height).

The highest scores on the third axis are for early standardized heights (0.539 for the protoconch, 0.408 for the fourth whorl), with protoconch width also scoring at 0.240. We do not understand the basis for associated high scores of umbilicus (0.320) and density of ribbing (0.358).

The smaller fourth and fifth axes express different aspects of the third allometric phase that builds *Cerion*'s aperture. The fourth axis records its two highest scores for measures of intensity in the change of orientation made by the growing edge before it deposits the definitive adult aperture (0.476 for apertural rotation, 0.435 for tilt). The fifth axis records the size of the expanded apertural mouth (0.443 and 0.317 for apertural height and width, associated with negative values for the penultimate whorl heights overgrown by this expansion, −0.245 and −0.352 for measures 16 and 17).

In summary, each axis makes sense in terms of both the general geometry of shell coiling (the whorl size versus whorl number principle for example), and the peculiarities of *Cerion*'s own universal pattern of growth (the apertural changes at adulthood, and the allometric compensation of flat top by later height, for example). We find interesting similarities and differences with patterns of covariation at the between-sample levels considered earlier. Dominating the within-sample system, we find two covariance sets that also regulate variation among mean vectors of *C. regina* samples—the compensatory shape covariance (setting axis one here), and the negative interaction of whorl size and number (expressed on both first and second axes). Most different from between-sample patterns are the greater strength of these two covariance sets, and absence of the general size factor that played an important role at all higher levels. Interestingly, these two differences are causally related. The size factor is absent here for the simple reason that size varies little among adults within most populations (length ranges from 27.0 to 34.0 mm in this sample), but greatly in mean values among populations (see appendix). The constraint covariance (whorl size versus whorl number) only operates when size ranges are small and restricted (see Gould and Paull, 1977 for quantitative demonstration)—for if adult size is free to vary, then large early whorls need not be compensated by growing fewer whorls to reach a limited final size.

To assess the generality of these within-sample covariances across taxa, we present, as Table 12, factor scores for the four large and interpretable axes (90.9% of information) of a *C. lewisi* sample (No. 221564, see appendix). The axes are remarkably similar to those noted just above in *C. regina*. High scores on the first axis emphasize *C. lewisi*'s chief character of many whorls and its consequence for slender shape (0.484 for whorl number, 0.323 for adult height, with adult width much less at 0.170, and 0.281 for height/width ratio of the adult shell). But we also note the constraint covariance, operating on this axis in the negative scores for standardized whorl sizes (−0.104 and −0.099 for protoconch and fourth width; −0.203 and

TABLE 12. SCORES FOR FOUR-AXIS SOLUTION OF SPECIMENS WITHIN A SAMPLE OF *C. LEWISI*.

	Measure	Axis 1	Axis 2	Axis 3	Axis 4
1.	PROWID	−0.104	0.362	−0.241	0.032
2.	FOURWID	−0.099	0.130	−0.185	0.171
3.	NUMWHO	0.484	−0.095	0.003	−0.024
4.	RIBDENS	0.344	0.284	0.434	0.133
5.	LENGTH	0.323	−0.050	−0.072	0.209
6.	WIDTH	0.170	−0.035	−0.209	0.140
7.	PROHT	0.048	0.330	0.210	0.140
8.	FOURHT	−0.203	0.454	−0.013	0.279
9.	FRSXHT	−0.178	0.315	−0.188	0.098
10.	UMBWID	0.036	0.309	0.143	0.014
11.	LIPWID	0.147	0.196	−0.324	−0.155
12.	LIPTHK	0.193	0.167	−0.042	−0.181
13.	APHT	0.123	−0.099	−0.240	0.306
14.	APWID	0.080	−0.155	−0.290	0.166
15.	APROT	−0.050	−0.109	−0.100	0.468
16.	EC	0.125	0.010	0.004	0.359
17.	FA	0.258	0.327	−0.119	−0.182
18.	APTILT	0.054	−0.092	0.023	0.430
19.	WEIGHT	0.208	0.036	−0.094	0.008
20.	HWRATIO	0.281	0.081	0.139	0.063
21.	PRORAT	−0.054	0.114	−0.437	−0.100
22.	FOURRAT	0.352	−0.011	−0.278	−0.153

−0.178 for fourth, and fourth to sixth whorl height).

The second axis, as did the third in *C. regina*, emphasizes standardized whorl sizes and little else. We are again puzzled that both ribbing (at 0.284) and umbilical width (at 0.309) also score strongly, for they did in *C. regina* as well, and we do not understand the basis for such an association—though its discovery in two taxa suggests a possible generality.

The third axis expresses the compensatory shape covariance that so dominates geographic sorting (both within and between islands) of *C. regina*, and also the first axis of within-sample covariation in *C. regina* sample 753. Its existence in *C. lewisi* supports our claim that this association is an important principle governing *Cerion*'s shape throughout the genus. The shell begins flat, with high score for protoconch width (−0.241) and opposite score for protoconch height (0.210—the factor loadings of all specimens are negative on this axis, so we discuss negative scores as high values). This initial flatness is recorded in high scores for width/height ratios of protoconch (−0.437) and fourth whorl (−0.278). But later heights compensate, and we note the continual gradient in scores for the three standardized heights that we have observed so many times before (+0.210, −0.013 and −0.188 for protoconch, fourth, and fourth to sixth whorls).

The fourth axis amalgamates the two apertural covariance sets that formed the fourth and fifth axes of *C. regina*. We note high scores for the two measures of change in orientation (0.468 for rotation, 0.430 for tilt) and for apertural size (0.306 for height, 0.166 for width).

The patterns of within-sample covariance for representative samples of two species are therefore similar to each other, and different from between-sample patterns in the same ways. In both, we find no general size axis since the within-sample range of shell size is small. In both, the compensatory shape covariance (flat top and later height) and the constraint covariance (whorl size versus whorl number) dominate the larger axes. The constraint

covariance appears more strongly in these within-sample patterns because it only operates when the range of final size is limited. In both samples, we also find sensible associations for measures of the aperture and standardized whorl sizes. We believe that we are here looking through a glass not so darkly at the general rules of growth within *Cerion*.

IX. Conclusion and Prospect

This work begins the second half of our long-term project to revise the Bahamian *Cerion* in the light of new data and contemporary concepts of evolution. It is our initial study, following our strategy of beginning with geographic outliers that maintain low diversity, of *Cerion* faunas in the southeastern Bahamas—a group of species different from those of Great and Little Bahama banks, the subjects of our previous work. We will move from here to the complexity of the largest island, Great Inagua, where more taxa (about 20) have been designated, and at least three widespread indigenous species actually exist.

A close relative of *C. regina* inhabits the long bank-edge northern coast of Great Inagua. But Inagua is big and diverse enough to maintain other indigenous *Cerion* species—including the vast populations of the island interior and bank-interior coasts (now called *C. rubicundum* and *C. dalli*, but probably belonging to a single species), and the widespread dwarfed *C.* (*Umbonis*) that lives in true sympatry (the first unambiguously recorded case in the entire genus *Cerion*) with both bank-edge and interior species. The small islands that we studied in the Turks and Caicos maintain only the bank-edge species as a widespread, indigenous form—but they permit us, by extension, to grasp the greater complexity of Inagua.

It is often said of historical sciences like ours (said, that is, by those who would degrade our activity, or bar us completely from the realm of science) that we traffic only in the narrative description of particulars and that we never predict or derive any generalities worthy of the name. Narrative must be treasured in its own right (for it can be every bit as factual as anything in science), but science must aspire to more—as historical science does, despite the caricatured dismissal outlined above.

The complexities and contingencies of history do preclude detailed prediction of future events, but prediction of this sort does not lie within our domain. Yet historical scientists work with a sort of prediction all the time—of events that have happened but have not yet been revealed by evidence, or of current situations inferred but not yet validated. In this essential component of generalization, natural historians work like all scientists.

Yet many of our subjects are so resolutely particular that we cannot proceed beyond simple narrative; thus, we must seek and exploit those situations of sufficient repetition to permit the apprehension of general pattern within the particulars. The attraction of *Cerion* lies in its central source of both narrative and generality—its overwhelming diversity, repeated in all ways that we can study: morphologically, genetically, biogeographically, ecologically.

Thus, we feel that we can creep to the end of an inferential limb and predict (based on genetic hints) that a second indigenous, geographically interior taxon may still persist (either as relatively pure populations or as substantial introgressed contributions to *C. regina*) in the centers of large islands on the Caicos Bank. We say this for two reasons: first, we have traced central distinctions between bank-edge and interior taxa on many other islands; second, we can often document the disappearance of the interior taxon on small islands that are, so to speak, "all" bank-edge, while the interior taxon persists on adjacent larger islands (for example, both bank-edge and interior *Cerion* live on Great Exuma, but only the bank-edge species on all the small adjacent cays). We also predict (based on repeated pattern from nearby Great Inagua), that should

this interior taxon be found, it will bear a smaller, thinner and more mottled shell than typical *C. regina* (we base this inference on the bank-edge versus interior distinction on all other islands, and particularly on the Inaguan separation between interior *C. rubicundum* and *C. columna*, the bank-edge analog of *C. regina*).

Likewise, our studies of allometry and ontogenetic covariance provide a basis for ordering variation within species (and often between hybridizing taxa) in a sensible way. The patterns dictated by what we have called the constraint and compensatory covariances are sensibly interpreted as necessary outcomes of *Cerion*'s basic ontogeny; they then determine the correlated consequences of any primary change in size or shape. And they occur over and over again in predictable manners and circumstances.

We find it intellectually satisfying that the primary component of narrative—*Cerion*'s buzzing and blooming outpouring of diversity—also becomes raw material for the repetitions that science requires for discussing general pattern. As great naturalists (G. E. Hutchinson, for example) exemplify by their life and work, exultation and explanation are complementary aspects of nature and its impact upon our minds.

LITERATURE CITED

AVISE, J. C., AND C. F. AQUADRO. 1982. A comparative summary of genetic distances in the vertebrates. Patterns and correlations. Evolutionary Biology, **15:** 151–185.

AYALA, F. J. 1983. Enzymes as taxonomic characters, pp. 3–26. *In* G. S. Oxford and D. Rollinson (eds.), Protein Polymorphism: Adaptive and Taxonomic Significance. New York, Academic Press.

CAIN, A. J., AND J. P. CURREY. 1963. Area effects in *Cepaea*. Heredity, **18:** 467–471.

CLENCH, W. J. 1937. Descriptions of new land and marine shells from the Bahama Islands. Proceedings of the New England Zoological Club, **16:** 17–26.

———. 1957. A catalogue of the Cerionidae (Mollusca-Pulmonata). Bulletin of the Museum of Comparative Zoology, **116:** 121–169.

———. 1961. Land and freshwater mollusks of Caicos, Turks, Ragged islands and the islands on the Cay Sal Bank, Bahamas. Occasional Papers on Mollusks, Museum of Comparative Zoology, Harvard Univ., **2**(26): 229–259.

CLENCH, W. J., AND C. G. AGUAYO. 1952. The *scalarinum* species complex (*Umbonis*) in the genus *Cerion*. Occasional Papers on Mollusks, Museum of Comparative Zoology, Harvard Univ., **1:** 413–440.

CRAMPTON, H. E. 1916. Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Tahiti. Carnegie Institute of Washington Publication, **228:** 1–311.

———. 1925. Studies on the variation, distribution, and evolution of *Partula*. The species of the Mariana Islands, Guam and Saipan. Carnegie Institute of Washington Publication, **228A:** 1–116.

———. 1932. Studies on the variation, distribution, and evolution of *Partula*. The species inhabiting Moorea. Carnegie Institute of Washington Publication, **410:** 1–335.

DEVRIES, W. 1974. Caribbean land molluscs: notes on Cerionidae. Studies Fauna Curaçao and other Caribbean Islands, **45:** 81–117.

GALLER, L., AND S. J. GOULD. 1979. The morphology of a "hybrid zone" in *Cerion*: variation, clines, and an ontogenetic relationship between two "species" in Cuba. Evolution, **33**(2): 714–727.

GOULD, S. J. 1969a. Character variation in two land snails from the Dutch Leeward Islands: geography, environment, and evolution. Systematic Zoology, **18:** 185–200.

———. 1969b. An evolutionary microcosm: Pleistocene and recent history of the land snail *P.* (*Poecilozonites*) in Bermuda. Bulletin of the Museum of Comparative Zoology, **138:** 407–532.

———. 1984a. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curaçao: a way of studying nonadaptation. Systematic Zoology, **33**(2): 217–237.

———. 1984b. Morphological channeling by structural constraint: convergence in styles of dwarfing and gigantism in *Cerion*, with a description of two new fossil species and a report on the discovery of the largest *Cerion*. Paleobiology, **10**(2): 172–194.

GOULD, S. J., AND C. PAULL. 1977. Natural history of *Cerion*. VII. Geographic variation in *Cerion* (Mollusca: Pulmonata) from the eastern end of its range (Hispaniola to the Virgin Islands): coherent patterns and taxonomic simplification. Breviora, **445:** 1–24.

GOULD, S. J., AND D. S. WOODRUFF. 1978. Natural history of *Cerion*. VIII. Little Bahama Bank—a revision based on genetics, morphometrics, and geographic distribution. Bulletin of the Museum of Comparative Zoology, **148**(8): 371–415.

———. 1986. Evolution and systematics of *Cerion* (Mollusca: Pulmonata) on New Providence Is-

land: a radical revision. Bulletin of the American Museum of Natural History, **182**(4): 389–490.

GOULD, S. J., N. D. YOUNG, AND B. KASSON. 1985. The consequences of being different: sinistral coiling in *Cerion*. Evolution, **39:** 1364–1379.

GULICK, J. T. 1905. Evolution racial and habitudinal. Carnegie Institute of Washington Publication, **25:** 1–269.

HUMMELINCK, P. W. 1940. Mollusks of the genera *Cerion* and *Tudora*. Studies Fauna Curaçao, Aruba, Bonaire and the Venezuelan Islands No. 5.

JOLICOEUR, P. 1963. The multivariate generalization of the allometry equation. Biometrics, **19:** 497–499.

———. 1984. Principal components, factor analysis, and multivariate allometry: a small-sample direction test. Biometrics, **40:** 685–690.

MAYNARD, C. J. 1889. Monograph of the genus *Strophia*. *In* Contributions to Science, vol. 1. Newtonville, Mass., self-published.

MAYNARD, C. J., AND N. A. CLAPP. 1919–26. Contributions to the history of the Cerionidae, with descriptions of many new species and notes on evolution in birds and plants. Appendix to vol. 10. Records of walks and talks with nature. West Newton, Mass., self-published, 242 pp.

MURRAY, J., AND B. CLARKE. 1980. The genus *Partula* on Moorea: speciation in progress. Proceedings of the Royal Society of London, **211:** 83–117.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics, **89:** 583–590.

PILSBRY, H. A., AND E. G. VANATTA. 1895. New species of the genus *Cerion*. Proceedings of the Academy of Natural Sciences of Philadelphia, pp. 206–210.

———. 1896. Catalogue of the species of *Cerion*, with descriptions of new forms. Proceedings of the Academy of Natural Sciences of Philadelphia, pp. 315–338.

RAUP, D. M. 1966. Geometric analysis of shell coiling: general problems. Journal of Paleontology, **40:** 1178–1190.

SELANDER, R. K., AND T. S. WHITTAM. 1983. Protein polymorphism and the genetic structure of populations. *In* M. Nei and R. K. Koehn (eds.), Evolution of Genes and Proteins. Sunderland, Mass., Sinauer Assoc.

SWOFFORD, D. L., AND R. B. SELANDER. 1981. BIOSYS-1. A Computer Program for the Analysis of Allelic Variation in Genetics. Users manual. Urbana, Univ. of Illinois, 65 pp.

WOODRUFF, D. S. 1975. Allozyme variation and genic heterozygosity in the Bahamian pulmonate snail *Cerion bendalli*. Malacological Review, **8:** 47–55.

———. 1981. Towards a genodynamics of hybrid zones. *In* W. D. Atchley and D. S. Woodruff (eds.), Essays on Speciation and Evolution in Honor of M. J. D. White. Cambridge, Cambridge Univ. Press.

WOODRUFF, D. S., AND S. J. GOULD. 1980. Geographic differentiation and speciation in *Cerion*: a preliminary discussion of patterns and processes. Biological Journal of the Linnean Society, London, **14:** 389–416.

———. 1987. Fifty years of interspecific hybridization: genetics and morphometrics of a controlled experiment involving the land snail *Cerion* in the Florida Keys. Evolution.

WRIGHT, S. 1978. Evolution and the Genetics of Populations, vol. 4, Variability within and among Natural Populations. Chicago, Univ. of Chicago Press.

APPENDIX: MATRIX OF MEANS FOR ALL SAMPLES.*

No.	Sample name	1 PROWID	2 FOURWID	3 NUMWHO	4 RIBDENS	5 LENGTH	6 WIDTH	7 PROHT	8 FOURHT	9 FRSXHT
1.	758T SC	53.00	74.00	7.806	12.75	30.85	12.00	21.25	58.30	70.40
2.	753A SC	53.00	75.50	7.898	13.88	30.81	12.29	21.69	57.06	67.94
3.	116022 SC	48.90	66.19	7.185	11.19	24.45	9.70	19.86	56.00	62.92
4.	189858 NC	57.50	72.05	7.506	12.63	27.17	10.36	25.90	65.65	63.50
5.	189859 MC	55.43	70.29	7.813	11.43	29.15	11.09	24.64	59.21	62.62
6.	219190 LC	52.80	76.35	7.588	13.30	29.21	12.04	21.50	57.45	71.37
7.	219192 GC	51.65	65.65	8.113	13.80	29.37	10.70	23.80	55.55	57.40
8.	219194 EC	55.00	74.00	7.698	12.71	31.33	11.90	24.50	58.08	71.75
9.	219195 GC	55.00	69.15	7.813	13.25	29.56	11.07	25.40	59.70	64.00
10.	219196 GC	52.70	68.85	7.400	14.40	27.02	10.51	21.95	60.20	63.85
11.	219197 EC	52.00	68.00	8.625	13.61	32.29	11.70	24.65	55.88	57.56
12.	219199 EC	53.06	71.19	7.477	15.50	27.31	10.69	20.94	57.88	65.88
13.	219200 EC	53.20	66.80	8.100	16.90	28.88	11.06	24.95	55.95	56.60
14.	219201 NC	51.20	61.05	8.544	17.65	29.25	9.96	26.15	55.05	49.90
15.	220898 LC	53.75	72.85	7.144	12.87	24.70	11.01	26.50	60.45	62.78
16.	220899 SAND	45.80	63.40	6.581	16.55	19.24	8.80	22.05	56.80	56.84
17.	220905 B	49.95	64.45	8.081	12.55	28.54	11.08	27.15	59.25	56.80
18.	220906 B	50.15	65.50	8.119	15.55	29.38	11.50	27.55	59.10	57.35
19.	220907 B	48.25	60.30	7.956	16.80	27.54	10.09	26.05	57.80	56.10
20.	220908 B	46.80	59.05	7.681	14.60	24.53	9.27	25.60	57.30	55.90
21.	220909 B	48.10	61.80	8.044	14.00	27.81	10.34	26.20	56.65	56.30
22.	220910 B	48.05	62.45	8.044	15.00	28.46	10.34	25.00	57.55	57.84
23.	220911 B	45.55	59.65	7.769	12.20	24.37	9.69	26.70	55.35	53.15
24.	220912 B	51.45	66.15	7.419	13.50	25.94	10.55	26.15	62.40	61.31
25.	220913 B	52.15	68.80	7.738	12.80	27.50	11.20	27.20	62.15	61.60
26.	220914 B	50.95	70.55	7.431	15.15	27.15	11.40	25.35	60.60	65.88
27.	221564 LPC	52.35	60.95	8.188	13.80	29.07	9.69	25.45	56.90	53.90
28.	221565 LFGC	49.70	56.60	8.031	15.65	25.36	8.70	25.25	54.55	48.89
29.	221566 LPARC	50.70	59.20	8.744	15.75	29.59	9.84	24.45	52.05	46.20
30.	221567 LWATC	55.60	64.55	7.831	12.50	28.21	9.94	26.00	58.95	59.16
31.	221568 LWC	49.78	60.11	7.306	15.22	22.21	8.79	25.78	56.11	50.40
32.	221569 LPR	48.08	57.20	7.790	13.88	25.36	8.54	23.84	55.08	53.45
33.	221570 LPR	53.40	62.00	8.138	14.40	27.12	9.32	25.30	56.80	52.60
34.	749 SC	51.20	69.45	7.756	11.72	28.38	11.22	22.00	54.65	63.05
35.	750 SC	52.00	69.60	7.500	11.29	27.44	10.57	21.35	57.05	66.24
36.	751 SC	50.70	68.60	7.588	10.00	27.16	10.71	20.85	53.10	64.20
37.	752 SC	52.10	71.15	7.300	11.26	26.05	10.67	20.45	56.20	64.54
38.	753 SC	54.10	77.40	7.888	11.25	32.09	12.84	20.55	55.85	68.15
39.	REG	56.95	70.15	7.094	12.30	25.79	9.98	25.40	65.35	62.17
40.	757 SC	52.63	74.16	7.803	13.21	30.71	12.18	20.32	55.16	69.53
41.	758 SC	53.15	73.95	7.906	12.15	30.94	11.91	21.30	58.15	67.50
42.	759 SC	53.25	72.85	7.756	11.16	30.11	11.83	21.15	56.90	67.75
43.	760 SC	50.20	69.05	7.881	13.11	28.52	11.38	19.75	52.65	62.50
44.	761 SC	50.05	70.55	7.731	15.05	28.10	10.93	20.55	55.05	64.30
45.	762 SC	48.95	64.40	7.400	10.90	24.94	9.67	20.00	53.75	62.29
46.	763 SC	49.33	64.53	7.683	15.13	26.55	10.15	20.67	52.80	62.47
47.	766 GT	53.33	76.11	7.944	10.11	32.08	12.41	24.44	63.11	67.00
48.	769 GT	51.30	77.20	7.688	14.10	29.67	11.70	24.30	62.00	69.75
49.	770 PR	58.00	73.25	7.619	15.10	28.83	11.08	26.80	63.95	64.75
50.	771 PR	59.40	71.90	7.519	16.30	28.40	10.63	27.90	66.20	64.83
51.	772 PR	51.70	65.40	7.575	15.21	26.14	10.16	23.80	57.45	61.63
52.	780 GT	52.25	75.10	7.419	13.05	28.14	11.31	24.50	64.75	68.36
53.	781 GT	52.35	70.90	8.244	13.80	31.38	11.80	25.25	59.70	63.20
54.	782 GT	54.75	73.15	8.094	13.30	30.32	11.97	27.00	62.90	61.25
55.	783 GT	55.15	75.75	8.125	13.45	32.64	12.41	25.20	63.00	66.15
56.	SCFOSIS	55.35	75.65	8.360		36.05	13.25	22.71	58.00	67.53

APPENDIX: CONTINUED.

10 UMBWID	11 LIPWID	12 LIPTHK	13 APHT	14 APWID	15 APROT	16 EC	17 FA	18 APTILT	19 WEIGHT	20 HW RATIO	21 PRORAT	22 FOUR-RAT
32.50	19.7	26.0	100.90	78.90	26.63	52.11	25.00	2.11	1.62	2.57	2.53	1.28
34.69	26.1	34.6	107.33	88.50	30.75	51.31	19.88	2.79	1.40	2.51	2.46	1.33
24.62	19.1	19.7	81.33	66.24	20.43	42.19	22.57	1.90	0.63	2.52	2.47	1.19
24.00	20.5	21.5	86.50	71.45	22.45	41.35	18.70	2.32	0.64	2.62	2.23	1.10
27.93	20.9	29.7	92.21	74.29	20.79	46.93	25.07	1.91	0.92	2.63	2.25	1.19
32.45	20.7	27.5	100.70	84.30	29.80	53.80	20.40	2.71	1.59	2.43	2.47	1.33
25.30	22.5	26.3	93.60	74.65	25.25	45.85	22.00	2.17	1.00	2.75	2.19	1.18
26.82	26.6	37.6	104.27	83.45	27.73	59.27	28.45	2.08	1.89	2.64	2.26	1.28
26.55	25.5	36.7	94.45	77.30	24.10	49.80	25.00	2.05	1.33	2.67	2.18	1.16
25.35	23.4	28.7	88.20	74.85	23.00	45.60	23.20	2.01	0.66	2.57	2.42	1.14
35.39	25.2	30.1	101.72	83.94	31.50	47.39	17.17	3.04	1.08	2.75	2.12	1.22
26.88	25.1	26.1	91.25	74.19	24.75	44.44	22.88	1.98	1.00	2.55	2.55	1.23
28.80	23.0	25.9	94.05	76.40	25.75	47.65	21.50	2.26	0.89	2.61	2.14	1.20
22.50	20.3	25.4	87.20	70.60	25.45	51.00	23.10	2.31	0.90	2.94	1.96	1.11
26.60	18.0	31.1	81.15	69.50	19.55	48.75	24.25	2.04	1.36	2.25	2.04	1.21
23.00	13.8	18.1	69.50	58.67	20.38	33.40	11.06	3.18	1.19	2.20	2.08	1.12
34.30	22.1	22.2	89.60	71.15	28.10	45.05	21.00	2.27	0.59	2.58	1.84	1.09
34.60	20.1	21.3	92.25	68.00	25.85	45.00	22.45	2.07	1.32	2.56	1.83	1.11
28.65	20.3	16.0	85.95	65.85	25.85	43.75	21.05	2.14	0.85	2.74	1.86	1.04
26.80	17.2	14.9	78.05	60.85	24.05	39.50	19.35	2.06	0.58	2.65	1.83	1.03
29.95	20.1	18.0	87.85	65.15	28.40	41.70	20.40	2.10	0.74	2.69	1.84	1.09
29.30	21.4	18.2	88.35	66.65	26.75	44.50	21.65	2.15	0.78	2.75	1.94	1.09
27.55	16.6	16.4	74.50	56.20	23.65	37.00	20.90	1.83	0.81	2.52	1.72	1.08
30.05	22.4	24.1	83.35	68.25	21.85	43.75	23.95	1.85	1.11	2.46	1.97	1.06
34.00	20.5	19.8	84.85	66.75	22.90	40.30	23.50	1.75	1.42	2.46	1.93	1.11
33.60	20.8	20.2	88.85	74.25	24.45	46.55	25.35	1.87	1.19	2.39	2.02	1.17
20.75	18.6	24.8	86.85	67.70	21.85	49.05	26.10	1.89	0.83	3.00	2.06	1.07
21.35	16.9	17.1	76.90	61.70	22.85	42.45	19.80	2.28	0.60	2.92	1.98	1.04
21.70	19.7	24.7	88.20	68.45	23.60	44.60	20.55	2.23	0.91	3.01	2.08	1.14
20.85	19.0	22.1	87.25	69.65	23.80	47.65	24.95	1.96	0.86	2.84	2.15	1.10
20.60	15.4	17.6	69.89	58.22	19.00	37.44	19.00	2.03	0.72	2.53	1.93	1.07
17.40	15.7	17.8	77.80	60.68	22.56	43.52	20.60	2.16	0.54	2.96	2.03	1.04
18.90	16.6	19.0	78.80	60.70	20.30	42.10	23.30	1.82	0.84	2.91	2.12	1.10
24.15	21.5	35.4	93.00	78.60	25.80	52.35	25.50	2.10	1.28	2.54	2.33	1.27
23.40	22.9	28.5	90.60	74.40	25.70	46.80	22.65	2.11	1.16	2.60	2.45	1.22
25.50	18.8	22.1	89.15	73.35	23.70	50.75	24.70	2.08	1.05	2.54	2.45	1.30
25.80	19.9	25.9	86.25	72.40	20.85	48.25	25.00	1.98	1.08	2.44	2.56	1.27
35.20	30.1	40.4	110.95	93.65	31.55	53.85	22.50	2.49	1.47	2.50	2.65	1.39
22.85	19.1	23.8	83.40	67.60	22.75	44.10	22.40	2.00	0.98	2.58	2.26	1.08
32.32	23.3	28.4	103.89	86.63	28.79	56.74	25.74	2.39	1.22	2.52	2.60	1.35
30.35	21.2	27.1	99.53	82.65	28.30	55.40	28.25	2.02	1.32	2.60	2.53	1.27
33.20	25.0	31.1	100.80	83.65	30.00	49.65	23.85	2.17	1.21	2.55	2.55	1.28
35.00	22.9	39.6	96.55	82.50	29.10	48.05	18.70	2.75	1.03	2.51	2.55	1.31
30.15	20.1	31.1	92.45	76.80	29.00	48.95	22.75	2.23	1.13	2.58	2.46	1.28
24.75	20.1	16.9	82.00	65.60	22.40	42.90	21.25	2.07	0.44	2.58	2.46	1.20
26.40	18.4	23.5	85.93	70.79	22.43	51.40	24.00	2.17	1.02	2.61	2.40	1.22
30.89	21.0	19.7	102.00	80.33	27.11	52.33	26.33	2.02	1.28	2.58	2.19	1.21
31.90	24.6	12.0	99.40	79.55	29.50	50.55	23.10	2.26	0.92	2.54	2.12	1.25
27.80	20.6	21.4	95.25	76.45	27.95	51.80	22.85	2.33	0.95	2.61	2.18	1.15
27.95	23.1	26.2	92.90	75.10	25.05	48.55	23.90	2.07	1.13	2.67	2.14	1.09
27.90	17.3	18.3	84.55	71.20	24.95	45.95	24.90	1.91	0.66	2.57	2.18	1.14
32.35	19.9	17.7	91.05	72.75	27.25	47.90	23.65	2.08	0.85	2.49	2.15	1.16
34.60	22.7	22.9	100.45	80.05	32.45	49.60	20.00	2.66	1.21	2.66	2.08	1.19
35.05	20.4	19.9	94.60	77.95	29.55	52.35	24.10	2.23	1.13	2.53	2.04	1.16
35.60	24.8	22.5	105.10	82.00	31.85	53.80	23.25	2.39	1.22	2.63	2.19	1.20
37.40	36.5	73.7	121.50	99.45	33.20	62.10	26.20	2.43		2.73	2.45	1.31

APPENDIX: CONTINUED.

No.	Sample name	1 PROWID	2 FOURWID	3 NUMWHO	4 RIBDENS	5 LENGTH	6 WIDTH	7 PROHT	8 FOURHT	9 FRSXHT
57.	SCFOSL	54.65	75.20	7.763		31.54	12.11	22.30	59.90	70.63
58.	754F SC	54.50	74.78	8.257		34.74	12.53	21.50	58.00	68.83
59.	756F SC	56.10	75.10	8.038		33.32	12.27	22.70	59.85	69.00
60.	765F SC	48.08	55.81	7.159		21.64	7.94	20.54	53.04	55.93
61.	768F GT	58.40	82.10	8.419		34.76	13.32	25.25	64.50	63.75

* Samples identified as follows: three digit numbers are our field localities; six digit numbers are catalogue designations for samples in the Department of Mollusks, Museum of Comparative Zoology. Suffixial letters as follows: B = *C. blandi*; L = *C. lewisi* (no special letter for *C. regina* samples); F = subfossil sample; SC = South Caicos; NC = North Caicos; MC = "Middle" Caicos; GC = Grand Caicos; EC = East Caicos; NC = North Caicos; WC = West Caicos; LC = Long Cay; SAND = Sand Cay; PR = Providenciales; GT = Grand Turk; PC = Pine Cay; FGC = Fort George Cay; PARC = Parrot Cay; WATC = Water Cay. The following special designations apply: locality 1, 758T, is the second sample (all from one tree) from locality 758; locality

APPENDIX: CONTINUED.

10 UMBWID	11 LIPWID	12 LIPTHK	13 APHT	14 APWID	15 APROT	16 EC	17 FA	18 APTILT	19 WEIGHT	20 HW RATIO	21 PRORAT	22 FOUR-RAT
32.85	27.3	39.2	105.40	86.15	28.40	57.05	26.45	2.21		2.60	2.47	1.26
33.05	35.3	57.6	115.89	93.85	33.35	58.50	26.50	2.27		2.78	2.57	1.29
32.05	29.7	46.8	110.60	87.50	29.65	56.00	27.10	2.09		2.71	2.50	1.26
18.19	14.7	13.2	68.12	54.73	20.73	40.73	19.69	2.09		2.70	2.37	1.06
39.20	25.4	27.0	108.80	87.25	31.15	58.10	28.05	2.13		2.61	2.33	1.27

2, 753A, is the second sample from locality 753; locality 39, REG, is a sample of *C. regina*, area unspecified; localities 56 and 57, SCFOSIS and SCFOSL, are two subfossil samples of *C. regina* from northeastern South Caicos. Units of measurement as follows: 1 and 7 (protoconch width and height) and 11 and 12 (lip width and thickness), in micrometer units, high power, at 18 units = 1 mm; measures 2, 8, 9, 10, 13, 14, 15, 16, 17 in micrometer units, low power, at 8 units = 1 mm; 3 and 4 are counts; 5 and 6 in mm by calipers; 19 in g by Mettler balance; 18, 20, 21, 22 are ratios.

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THE NEOTROPICAL ORB-WEAVING SPIDERS OF THE GENUS *ALPAIDA* (ARANEAE: ARANEIDAE)

HERBERT W. LEVI

ABSTRACT. *Alpaida* species are diurnal orb-weavers with diverse habits and diverse webs. They are known from the Neotropics only. Adult *A. quadrilorata* are reported to be associated with a certain plant species and, when disturbed, dive into a pool of rainwater at the base of its leaves. Perhaps other species have similar specific habits.

Alpaida is related to *Edricus* based on the structure of the genitalia, but differs by the glabrous brightly colored body and from most araneids by the fusion of radix, embolus and terminal apophysis and by the presence of a paramedian apophysis in the male palpus.

There are 134 known species, 40 previously known, 94 new. That is, fewer than 30% had previously been known, the same proportion as in my 1986 revision of *Chrysometa*. There are 25 new synonyms. The 40 previously known species had been placed incorrectly in 12 different genera, many of the genera not otherwise represented in the Neotropics. The names of the four common, widespread species *A. bicornuta*, *A. leucogramma*, *A. truncata* and *A. veniliae* had 13 synonyms; these species had previously been known under a total of 17 names in various areas.

INTRODUCTION

Alpaida is a large genus and may eventually contain 200 to 300 species. There are no distinct species groups and it would be difficult to split the genus, except by taking one or two species out. But the size of genera is controversial and subjective. In other animal groups (e.g., birds) a large number of genera has not been of help in indicating relationships, nor does it contribute to the stability of names (Levi, 1973: 474). A practical aspect of this issue is the need for museum staff to be able to recognize genera in incoming collections, sort them out and make them available for study. Those spider families with the most numerous genera (Salticidae and Linyphiidae) remain the most neglected, and splitting of genera into groups with only one or two species would not make their study more manageable.

The genus *Alpaida* in Bonnet's catalog (not Roewer's) contains only one species, although it is here seen to be one of the largest neotropical araneid genera, including many common species. On the basis of superficial similarities, the known *Alpaida* species had previously been described and assigned such diverse generic names as *Araneus* (*Epeira*, *Aranea*), *Cercidia*, *Drexilia*, *Edricus*, *Epeirella*, *Lariniacantha*, *Metepeira*, *Miranda*, *Salassina*, *Singa*, *Verrucosa* and *Wixia*.

Seventy % of the *Alpaida* species are new. This is a much larger percentage than anticipated and is comparable with the number of new species of *Chrysometa* (Levi, 1986). If other neotropical araneid genera have a similar percentage of new species, I will have greatly underestimated the total number of neotropical species.

MATERIALS AND ACKNOWLEDGMENTS

Any revision depends on reference to far-flung materials and is possible only with the assistance of many cooperators. I am grateful to the curators who made collections available. In many cases, huge collections of valuable specimens were entrusted to the mails. The following list identifies the collections used; abbreviations for the institutions are mostly the standardized ones (Leviton et al., 1985), and private collections are listed by the initials of the owner.

(AMNH) American Museum of Natural History, New York, N. Platnick;
(BMNH) British Museum (Natural History), P. Hillyard, F. Wanless;
(CAS) California Academy of Sciences, W. J. Pulawski, D. Ubick;
(CUC) Cornell University collections kept in the AMNH, N. Platnick;
(DU) D. Ubick;
(IRSNB) Institut Royal des Sciences Naturelles de Belgique, Brussels, L. Baert;
(MACN) Museo Argentino de Ciencias Naturales, Buenos Aires, E. A. Maury;
(MCN) Museu de Ciencias Naturais, Porto Alegre, A. Lise, E. Buckup;
(MCZ) Museum of Comparative Zoology;
(MECN) Museo Ecuadoriana de Ciencias Naturales, Quito, L. Avilés;
(MEG) M. E. Galiano;
(MHNG) Museum d'Histoire Naturelle, Genève, V. Mahnert;
(MHNM) Museo de Historia Natural de Montevideo, R. M. Capocasale;
(MIUP) Museo de Invertebrados, Universidad de Panamá, Panama, D. Quintero A.;
(MLP) Museo de Universidad Nacional, La Plata, R. F. Arrozpide;
(MNHN) Museum National d'Histoire Naturelle, Paris, J. Heurtault, J. Kovoor;
(MNHNP) Inventario Biológia Nacional, Museo Nacional de Historia Natural, Asunción, J. Kochalka;
(MNRJ) Museu Nacional, Rio de Janeiro, A. Timotheo da Costa;
(MZSP) Museu de Zoologia da Universidade de São Paulo, P. Vanzolini, L. Neme, J. L. M. Leme;
(MZUF) Museo Zoologico, Università, Florence, S. Mascherini;
(MZUT) Museu ed Istituto du Zoologia Sistematica, Universita di Torino, O. Elter;
(NHRM) Naturhistoriska Riksmuseet, Stockholm, T. Kronestedt;
(NMB) Naturhistorisches Museum, Basel, E. Sutter;
(PAN) Polska Akademia Nauk, Warszawa, A. Riedel, W. Staręga, J. Proszynski, A. Slojewska;
(REL) R. E. Leech;
(SMF) Forschungsinstitut Senckenberg, Frankfurt, M. Grasshoff;
(USNM) National Museum of Natural History, Smithsonian Institution, Washington, J. Coddington;
(ZMB) Zoologisches Museum der Humboldt Universität, Berlin, M. Moritz;
(ZMK) Zoologisk Museum, København, H. Enghoff;
(ZSM) Zoologisches Staatsmuseum, Munich.

The collections of Maria Elena Galiano used are now deposited in MACN. An attempt was made to deposit types of names in the country where collected in museums that can make the specimens available.

Numerous collectors supplied specimens and notes. Especially important information on habits and habitats came from the collections of W. Eberhard, W. Maddison, D. Smith and J. Kochalka. J. Gruber and P. Vanzolini provided information on localities; A. A. Lise provided needed literature. L. R. Levi and D. Woessner read and improved the wording. J. Coddington made numerous suggestions for the manuscript. C. Villars, S. Hunt and D. Woessner typed various drafts. The research was supported in part by National Science

Foundation grant BSR 83 12772. Publication costs of this study were covered in part by the Wetmore Colles Fund.

METHODS

The methods of this revision are the same as used for previous studies (Levi, 1985, 1986). The internal female genitalia are not illustrated as two views of the outside of the epigynum, and the color pattern and the shape of the abdomen are sufficient in *Alpaida* to separate the females. The palps are illustrated in mesal view only, with the cymbium on the left and median apophysis and terminal apophysis showing.

I indicated the specimens that were described and illustrated. But illustrations were often improved after finding lightly sclerotized specimens that showed seams or structures not seen in the original specimen.

Males were matched with females by their appearance and by matching their collecting sites, but this has been difficult and errors may have been made.

Because specimen labels are frequently very old and handwritten, difficulties are commonly encountered in finding localities in gazetteers and on maps. Often there is no country or province given and there may be misspellings; in some cases spellings or names of localities have changed, some settlements have disappeared or there may be several localities with the same name. The gazetters listed in Levi (1985) and our collection of maps have been most useful. Some errors in placing localities in my past revisions were noticed.

The type specimens of names were examined over a period of 20 years. Since it was more important at the time to make illustrations and make certain that all syntypes of a name were the same species, I often neglected recording their number. Lectotypes are only designated when a mixture of species is suspected, not as a routine.

Alpaida O. P.-Cambridge

Alpaida O. P.-Cambridge, 1889: 52. Type species by monotypy *A. conica*. Levi, 1976: 388. The name is feminine.

Parepeira Mello-Leitão, 1933: 41. Type species *Epeira albostriata* Keyserling (=*A. leucogramma*).

Subaraneus Caporiacco, 1948: 661. Type species by original designation *Epeira veniliae* Keyserling (=*A. veniliae*).

Lariniacantha Archer, 1951: 15. Type species by original designation *Epeira grayi* Blackwall (= *A. grayi*).

Subedricus Caporiacco, 1954: 84. Type species by original designation *Epeira nigropostulata* O. P.-Cambridge (=*A. truncata*).

Note. I synonymized several generic names in 1976, but find now that *A. calix* Walckenaer, redescribed and illustrated in 1976, does not belong in the genus. It lacks the characteristic paramedian apophysis in the male palpus, and the terminal apophysis is a thin blade attached on hematodocha and lying parallel to the embolus (Levi, 1976: 389, figs. 143, 144), rather than the large sclerotized structure fused to embolus and radix found in *Alpaida*. It belongs with some other neotropical species in a new genus yet to be named.

Diagnosis. Alpaida species are recognized by the glabrous body, orange carapace (sometimes with dark pattern), and, in females, by the wide head with eyes ringed in black (Fig. 2). The black eye rings are not drawn out anteriorly and posteriorly as in *Araneus* species. In most species I have seen alive, the abdomen has red, green, yellow and orange colors that wash out in alcohol. The epigynum is usually a transverse sclerotized structure, with posterior lips, its middle portion drawn out into a triangular lobe or scape (Fig. 7). In posterior view there is a median plate framed by a lip (Fig. 8). The openings are on each side between plate and lips. In many species the lobe or scape is broken off in the course of mating (Figs. 149, 150). The epigynum is simpler and shorter than that of *Edricus* (?=*Wagneriana*). (At present, I do not know the correct name for the group which includes *Wagneriana tauricornis*.)

The male has a narrow head (Fig. 5). The palpus has the radix, embolus and terminal apophysis fused into one sclerite (Fig. 10), a character not seen in other araneid genera. In both *Alpaida* and *Edricus*, the palpus has a mushroom-shaped paramedian apophysis (Fig. 10), its top showing between the cymbium and embolus (Figs. 10, 43, 56). The stalk of the paramedian apophysis is attached to the conductor. *Alpaida* males differ from *Edricus* males by having a glabrous orange carapace, sometimes with a dark pattern on the head, while the male of *Edricus* is hirsute with an orange head and the sides of the carapace darker. The palpus of the *Edricus* male has a much larger, more complex median apophysis (Levi, 1976, figs. 69, 70) than has the palpus of *Alpaida*.

Alpaida is separated from the glabrous species of *Metazygia* and *Mangora* by the structure of the genitalia (see below); also, females of *Mangora* have a narrower head and *Mangora* males and females both have feathered trichobothria on the third tibiae.

Description of female. Color. The carapace is usually orange, sometimes yellowish, often with a black or dark brown pattern on the head. The eyes are always ringed by black; often the entire median ocular area is black (Fig. 41). The labium and endites are orange to black; the sternum is orange or black; the coxae are sometimes black, but more often light orange, sometimes contrasting with the sternum and more distal leg articles. The distal leg articles are uniform yellow to orange or have dark rings. In live spiders, the abdomen has greens, reds and yellows that wash out in alcohol, leaving white and black pigment (Plate 1). In specimens stored in alcohol, the venter may be uniformly dark or light orangish-gray; often there is a light longitudinal line on each side and almost always a pair of white pigment spots on each side of the spinnerets. The spinnerets are usually darker than the venter of the abdomen.

Structure. The carapace lacks hairs, or has only a few (with some exceptions). The head is wide and bulging, with the median eyes on a slight hump (often all black), and the lateral eyes on a joined black tubercle. Usually all eight eyes are subequal in size or the lateral eyes are slightly smaller than the medians; in a few species the posterior median eyes are larger than the others and rarely the anterior median eyes are largest. Anterior medians and posterior medians are about their diameter apart and more than their diameter from the laterals. The thoracic depression is shallow. The chelicerae are strong and armed with three or four teeth on each margin. The first legs are usually the longest and in some species the fourth legs are slightly longer than the first. The abdomen shape is diverse, almost always longer than wide, rarely spherical, often with shoulder humps, an anterior median hump, or posterior humps, or drawn out posteriorly; rarely with lateral lobes (Figs. 328, 493). The abdomen sometimes has one to four pairs of slightly sclerotized thorns or spines, or an anterior median spine (Figs. 13, 71, 73). Many species seem to have paired lateral humps when the abdomen is emaciated, but the lobes do not show when the abdomen is full (Figs. 369, 370).

Description of Male. Color. Coloration of males is as in females, with the abdomen pattern less distinct.

Structure. Unlike most other araneids, *Alpaida* males often have the carapace larger than that of females and sometimes the total length of the body is longer (Figs. 42, 202). The male's head is narrow in front, unlike the female's, and there is a longitudinal thoracic line with a short posteriorly directed branch on each side in the middle (Fig. 5). The chelicerae are smaller than those of females (Figs. 4, 6). The endite always has a tooth facing a tooth on the palpal femur. The first coxa has a hook that fits into a groove on the second femur (Fig. 6); the hook and groove are lacking only in *A. delicata*. The fourth coxae or trochanters may be armed with short stout macrosetae. The second tibiae are the same thickness as the first or only slightly thicker, with a few indistinct macrosetae. *Alpaida truncta* has the second

Plate 1. Upper left, female *Alpaida graphica,* carapace orange, abdomen blueish black, 8 mm total length. Upper right, female *A. bicornuta,* carapace orange, abdomen with yellow-white patches on orange; tips of spines, posterior tip and sides black, 5 mm total length. Lower left, female *A. truncata,* carapace and legs orange-yellow, abdomen yellow with black patches, 8 mm total length. Lower right, immature *A. quadrilorata,* orange with black patches, 6 mm total length. (photo upper left W. Maddison, upper right J. Coddington.)

tibia modified (Fig. 578), and *A. delicata* has the distal ends of the first and second tibia swollen and armed with macrosetae (Fig. 478). (The anatomical differences of *A. delicata* are expected to reflect differences in mating behavior, a promising research project.)

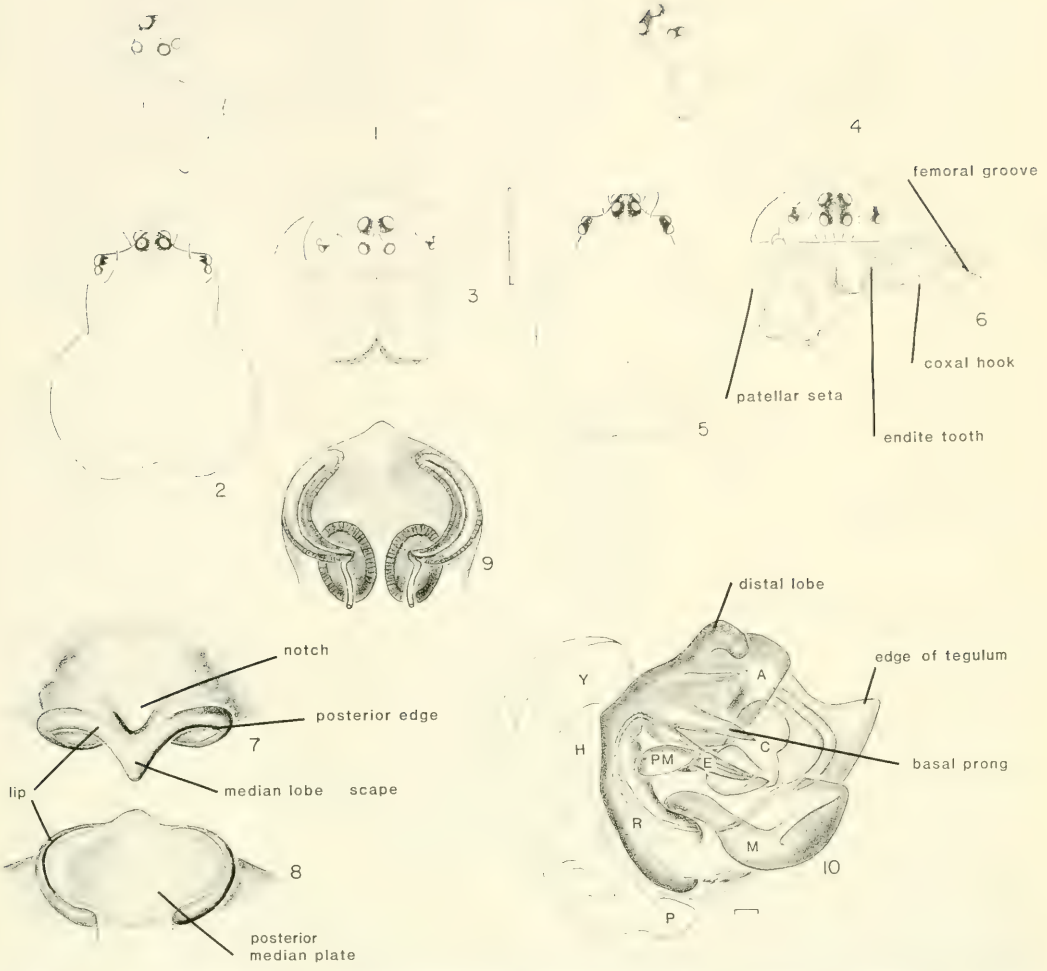
The palpal femur has a basal tooth fac-

ing the tooth on the endite (Fig. 6). The palpal patella has at least one long macroseta (Fig. 6); several species (*chickeringi, almada, grayi*) have two. The palpal tibia has a slight bulge on one side underneath the median apophysis (Figs. 18, 30). The palpal tibia of *A. delicata* has the characteristic bulge, but is longer than wide (Fig. 477), as is usual in Tetragnathidae, but unusual in the Araneidae. The cymbium is not modified, but the paracymbium may be more elaborate than a hook (this character was not examined in detail because it shows only at a difficult-to-repeat angle from "below" the palpus). That the cymbium never has a tarsal organ is easily seen in *Alpaida* because there are fewer setae than in other Araneidae. The median apophysis (M in Fig. 10) is smaller than that of *Edricus* and usually elongate, often with a blunt tooth at the end toward the cymbium, sometimes with a keel. The median apophysis never has sharp spines or the flagella found in species of genera related to *Araneus* (listed below). The axis of the radix (R in Fig. 10) is often nearly parallel to that of the cymbium. The embolus is knife-blade shaped and similar in many species (E in Fig. 10); in only a few species is it curved (Fig. 215) or filiform (Fig. 592). The tip of the embolus is always supported by the conductor (C in Fig. 10). The conductor is large, complex, and has the mushroom-shaped paramedian apophysis attached to its base (PM in Fig. 10). The attachment is hidden by the embolus. The complex, often very large terminal apophysis (A in Fig. 10) is fused with the embolus, without a joint or distal hematodocha. Terminal apophysis and embolus are fused with the radix (R in Fig. 10); if separated and broken off, the conductor and median apophysis also come off as the conductor is fastened only by a stalk to the tegulum and the median apophysis by an hematodocha. (The fusion of sclerites was checked in the larger species and also in *A. anchicaya, conica, delicata, tuonabo* and *chickeringi*. The male of *A. murtinho* has a joint between the radix and embolus-terminal apophysis.)

Relationship. The presence of a paramedian apophysis in the palpus, the lack of pointed spines on the median apophysis and the reduction or lack of distal hematodocha place this genus into a group with *Eriophora, Verrucosa, Acanthepeira, Edricus, Cyclosa, Wixia, Micrathena, Chaetacis* and *Gasteracantha*. I consider these characters synapomorphies of the group. *Scoloderus* and *Acacesia* have a similar median apophysis and lack of distal hematodocha, but are distinct in lacking a paramedian apophysis, perhaps a secondary loss. In contrast, *Araneus, Mangora, Nuctenea* (=*Larinioides*), *Neoscona, Aculepeira, Cercidia, Kaira, Larinia, Singa, Eustala, Metazygia* and *Metepeira* lack the paramedian apophysis and have a distal hematodocha between embolus and terminal apophysis. Both characters are probably synapomorphies for these genera. *Edricus* (?=*Wagneriana*) shares with *Alpaida* the peculiar mushroom-shape of the paramedian apophysis, a synapomorphy of the two sister genera.

Since a number of genera have genitalic structures similar to those of *Alpaida*, a study of what is primitive or specialized in these groups will be postponed until a later time as this paper is one of a series on related groups. Also more on the relationship with other genera will be learned after a second look at *Araneus* and genera not close to *Alpaida*.

Natural History. Webs and habits are more diverse than in species of other araneid genera. W. Eberhard (in personal communication) summarizes *Alpaida* webs: "Webs are generally more or less vertical, but vary widely in design. In some species the spider rests facing away from the orb in a curled leaf and monitors a signal line running to the hub (e.g., *A. truncata*, Plate 2). In others (e.g., *A. acuta*, Plate 2) there is no curled leaf, but a signal line runs to the spider, which rests on the substrate (e.g., tree trunk). In others (e.g., *A. tuonabo*), webs are built far from any substrate, and the spider rests at the hub (head downward) except when it has an egg-sac; in this case the orb is smaller and



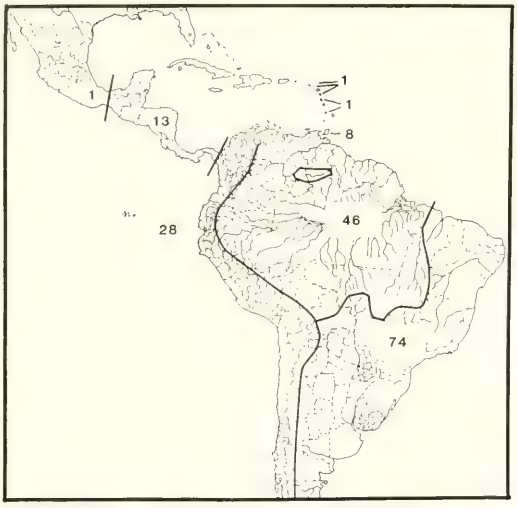
Figures 1–10. *Alpaida* morphology. 1–3, female carapace and chelicerae. 4–6, male. 1, 4, lateral. 2, 5, dorsal. 3, 6, frontal. 6, with left palpus. 7–9, female epigynum. 7, ventral. 8, posterior. 9, posterior, cleared. 10, left male palpus, expanded. Figs. 1–6, *A. leucogramma.* 7, 8, diagrammatic. 9, *A. bicornuta.* 10, *A. grayi.*

Scale lines. 1.0 mm, except Figs. 9, 10, 0.1 mm.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; H, basal hematodocha; M, median apophysis; P, paracymbium; R, radix; Y, cymbium; PM, paramedian apophysis.

has fewer radii and spiral loops, and a line runs from the hub to the sac (usually a leaf) where the spider sits. In contrast to the previous species, *A. leucogramma* make webs close to the ground (hub usually less than 20 cm from the ground) and the spider rests facing downward at the hub and falls to the ground readily when disturbed. Habitats range from deep forest to open lawns. Some species (e.g., *A. tuonabo*) readily replace webs immediately after rains, others (e.g., *A. truncata*) do so much less readily."

More information is provided under the species description of more common species (*bicornuta*, *carminea*, *quadrilorata*, *truncata*, *tuonabo* and *veniliae*). *A. quadrilorata* seems limited to one species



Map 1. The number of species of *Alpaida* in different areas.

of plant and when disturbed drops into a water puddle at the base of the leaf (J. Kochalka, letter).

A specimen of *A. alvarengai* has the right fourth leg regenerated. (Regeneration is uncommon in the family.)

The median lobe of the epigynum of a number of species readily breaks off, probably preventing a second mating.

Shelly (1983) observed webs and prey selection of *Alpaida tuonabo* and most appears known about this species. Some of Shelly's observations are summarized below with *A. tuonabo*. There is some indication that the niche of *Alpaida* is much narrower than of other orb weavers. For instance, *A. quadrilorata* has been collected from the thistle-like umbellifer *Eryngium horridum*. Are adults always found on this plant? *Alpaida graphica* is associated with small sink-holes in the Yucatan peninsula. Do others have similar restricted habitats?

Alpaida species are limited to the Neotropics. Only one species (*A. septemmammata*) has been found north of the Isthmus of Tehuantepec; 13 species occur in Central America. While eight species have been found on Trinidad, larger islands of the Lesser Antilles have one species each and *Alpaida* is absent from the Greater Antilles. About 28 species have been found on the western slope of the Andes, and about 46 are found in the Amazon and Orinoco drainage area; the largest number, about 74, are found in eastern South America (Map 1).

Alpaida

Key to Females

(Terms used in this key are illustrated by Figs. 7 and 8.)

1. Abdomen with spines or pointed tubercles (Figs. 13, 65, 269, 276, 637) 2
– Abdomen without spines, sometimes with blunt tubercles (Figs. 206, 326, 488, 493) 14
2(1). Abdomen with anterior median spine (Figs. 65, 71, 82, 212) 3
– Abdomen without anterior median spine (Figs. 13, 15, 276, 630) 7
3(2). Abdomen with 5 spines (Fig. 82); Guyana (Map 2). ..... *kartabo*
– Abdomen with 1 or 3 spines (Figs. 65, 212) 4
4(3). Anterior median spine much larger than laterals (Fig. 212) (laterals may be absent), abdomen without dorsal longitudinal markings (Figs. 212, 213); lower Amazon area (Map 3) ..... *manicata*
– Three spines subequal, abdomen with dorsal longitudinal bands or markings (Figs. 65, 71, 77) 5
5(4). Median spine anterior to laterals (Fig. 65); median lobe of epigynum framed by lateral lobes (Fig. 63); widespread Panama to Argentina (Map 2) ..... *trispinosa*
– All 3 spines in a row (Figs. 71, 77); epigynum otherwise (Figs. 69, 75) 6
6(5). Median lobe of epigynum pointed (Fig. 69); posterior median plate without dorsal lobes (Fig. 70); abdomen with bands (Fig. 71); southeastern Brazil (Map 2) ..... *keyserlingi*
– Median lobe of epigynum rounded (Fig. 75); posterior median plate with lateral dorsal lobe (Fig. 76); abdomen with indistinct dorsal bands (Fig. 77); Peru (Map 2) ..... *monzon*
7(2). Abdomen oval, pointed posteriorly with a pair of shoulder spines (Figs. 13, 263, 276) 8
– Abdomen with lateral humps and minute pair or pairs of spines on humps (Figs. 630, 637, 642) 12
8(7). Epigynum longer than wide in sub-

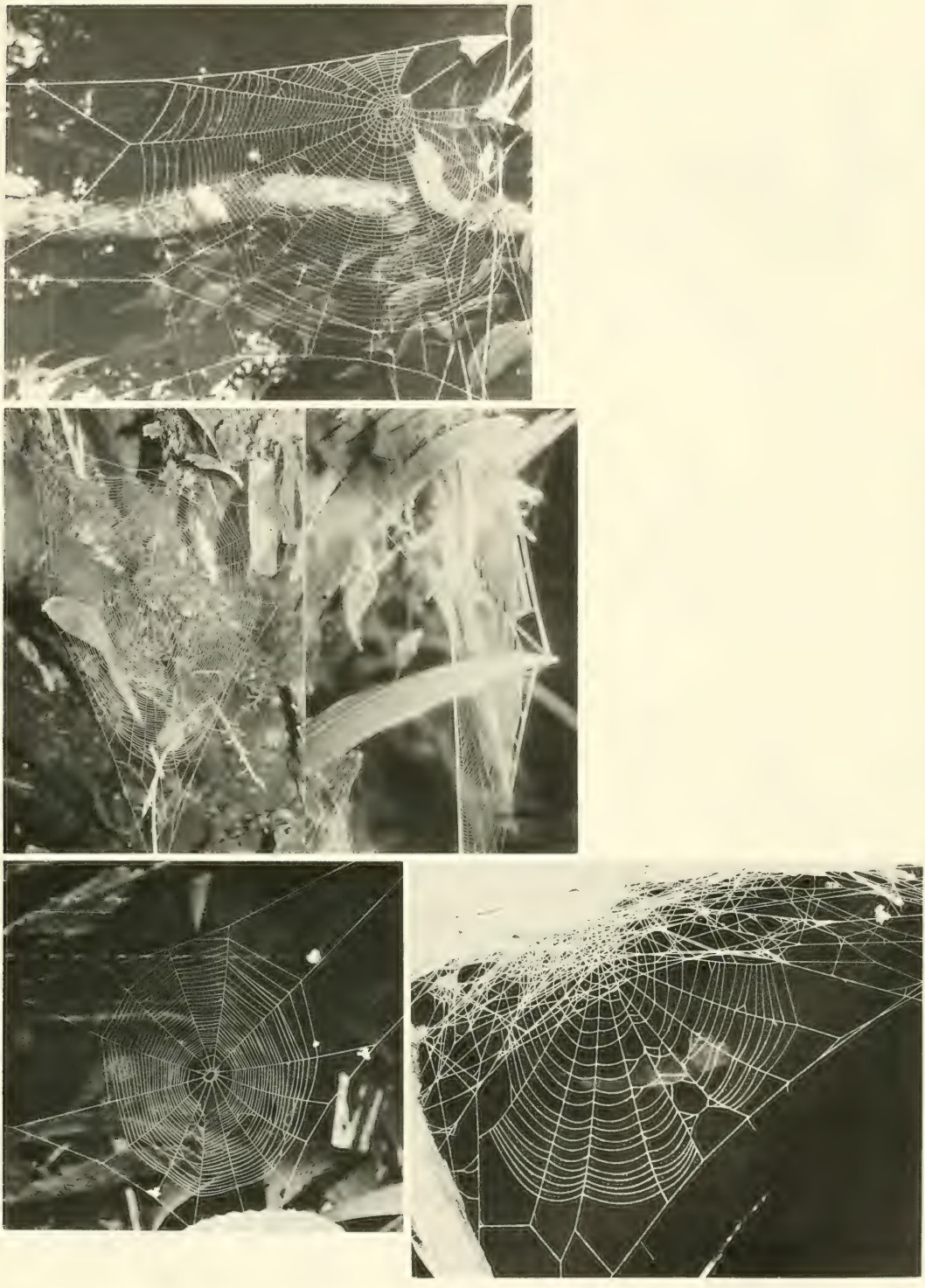
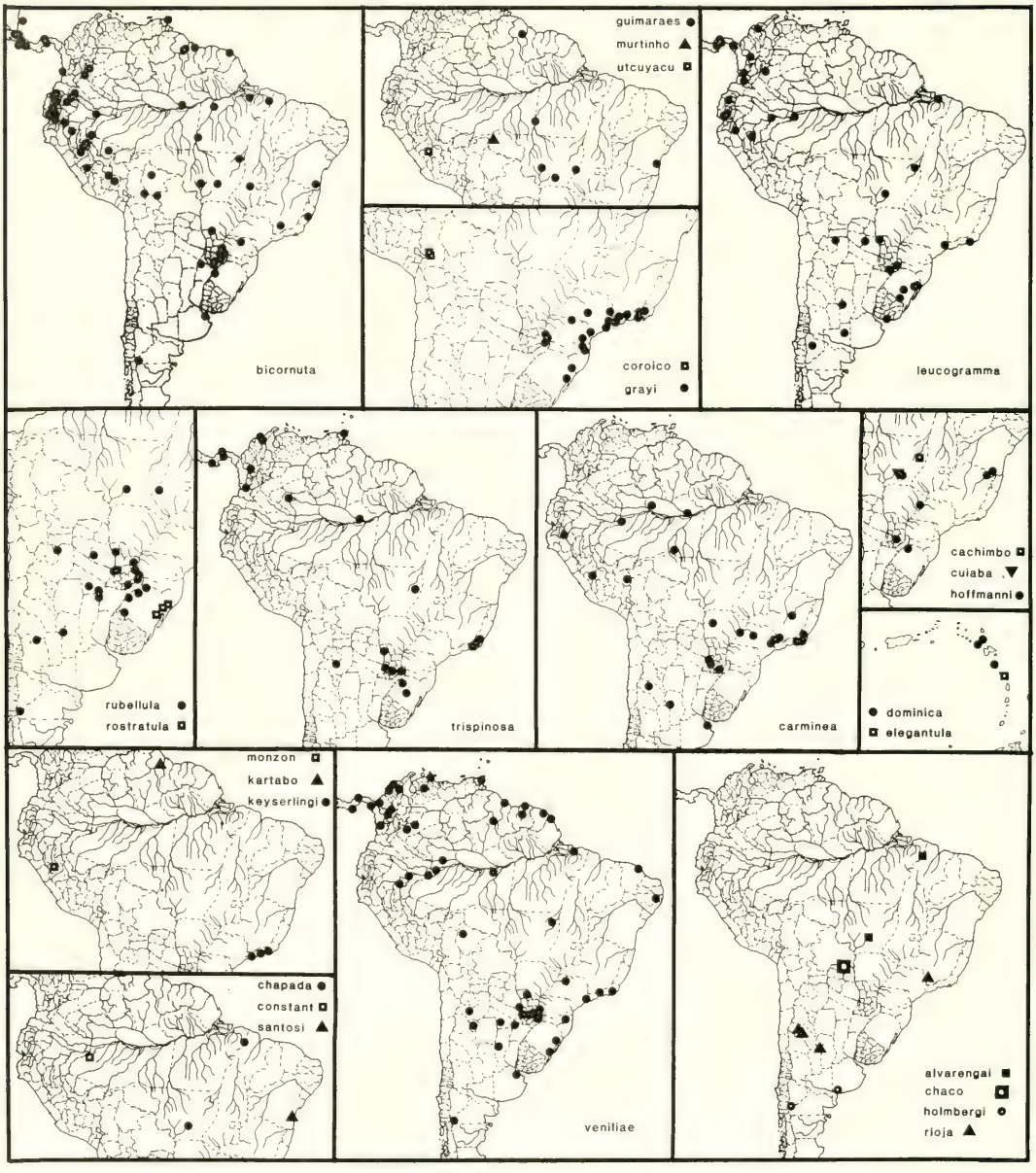


Plate 2. *Alpaida* web diversity. Webs of adult females. Top, *A. truncata*, maximum diameter of sticky spiral 18.7 cm. Middle, *A. moata*, maximum vertical diameter of sticky spiral 17.1 cm. Bottom left, *A. championi*, max. diameter of sticky spiral 18.2 cm. Right, *A. acuta*, center to bottom spiral 9 cm. (All photographs W. Eberhard.)



Map 2. Distribution of *Alpaida* species.

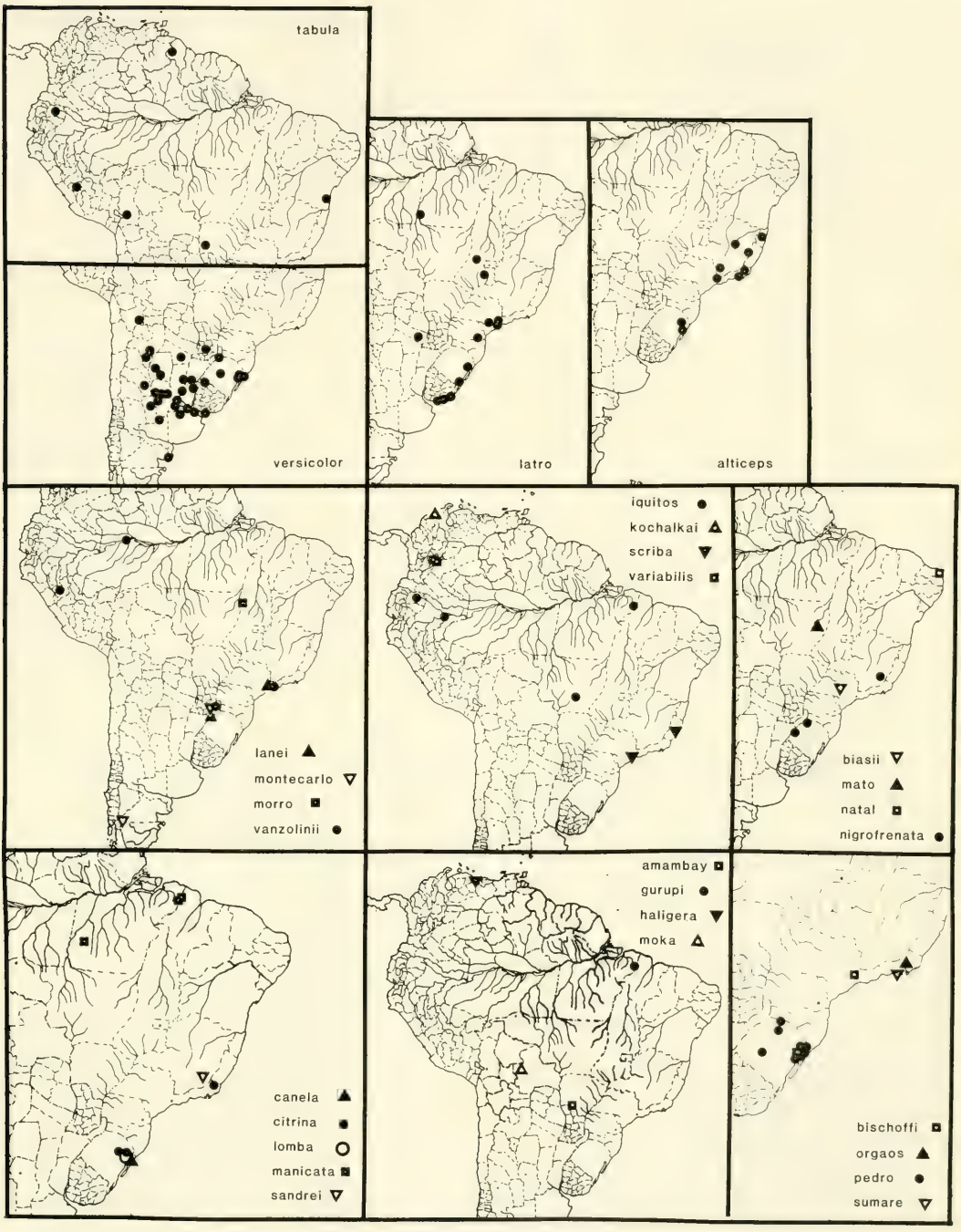
ventral and posterior view (Figs. 261, 262); central Ecuador (Map 4) ..... *banos*

– Epigynum wider than long (Figs. 11, 12, 271, 272) 9

9(8). Epigynum in ventral view with larger triangular lobe and median longitudinal light band (Fig. 11); posterior median plate oval without lobes (Fig. 12); widespread, Central America to central Argentina (Map 2). ..... *bicornuta*

– Epigynum otherwise (Figs. 267, 271, 274) 10

10(9). Epigynum with a large triangular



Map 3. Distribution of *Alpaida* species.

notch, tip of notch in line with posterior edge (Fig. 271); southwestern Colombia (Map 4) ..... *narino*

– Epigynum otherwise (Figs. 267, 274) 11

11(10). Abdomen constricted posterior to its lateral spines (Fig. 276); Mato Grosso, Brazil (Map 3) ..... *amambay*

– Abdomen not so constricted, spines dorsal (Fig. 269); northeastern Ecuador (Map 4) ..... *cuyabeno*

12(7). Epigynum with a transverse lip (Fig. 640), epigynum wider than long in posterior view (Fig. 641); French Guiana (Map 5) ..... *sulphurea*

– Epigynum otherwise and as long as wide (Figs. 628, 635) 13

13(12). Posterior median plate constricted in middle (Fig. 629); Panama, southern Colombia to Guyana (Map 5) ..... *chickeringi*

– Posterior median plate oval (Fig. 636); southwestern Colombia (Map 5) ..... *almada*

14(1). Epigynum square, or longer than wide in subventral view (Figs. 103, 122, 154, 515, 541) and square to longer than wide in posterior view (Figs. 105, 123, 155, 516, 542) 15

– Epigynum wider than long in ventral or posterior view (Figs. 19, 20, 253, 254) 28

15(14). Transverse notch anterior to the posterior edge of the epigynum (Fig. 446); epigynum triangular in posterior view (Fig. 447); Guatemala to southwestern Colombia (Map 4) ..... *championi*

– Epigynum otherwise 16

16(15). Epigynum with an anterior edge (Fig. 555); Colombia (Map 5) ..... *eberhardi*

– Epigynum without distinct anterior edge 17

17(16). Epigynum with a scape slightly constricted proximally (Fig. 541); northern Colombia (Map 5) ..... *darlingtoni*

– Epigynum otherwise 18

18(17). Epigynum with heartshaped posterior median plate (Fig. 516); abdomen with small anterior median hump and narrow posterior point (Fig. 517); Buenos Aires Prov., Argentina (Map 5) ..... *costai*

– Epigynum otherwise; abdomen oval, without anterior median hump (Figs. 124, 595) 19

19(18). Scape (or median lobe) larger than base of epigynum (Figs. 587, 593, 599) 20

– Median lobe (scape) indistinct, or distinctly set off and small; sides of epigynum more or less parallel (Figs. 103, 122, 154, 198, 605) 22

20(19). Tip of scape rounded (Fig. 593); abdomen elongate (Fig. 595); Panama (Map 5) ..... *tuonabo*

– Tip of scape pointed (Figs. 587, 599); abdomen oval (Figs. 589, 601) 21

21(20). Epigynum with a pair of dark patches in posterior view (Fig. 600); western Colombia to Ecuador (Map 5). ..... *cisneros*

– Epigynum with a pair of indistinct dorsal notches in posterior view (Fig. 588); southwestern Colombia (Map 5) ..... *anchicaya*

22(19). Dorsum of abdomen with paired black patches (Fig. 106); posterior median plate convex with parallel sides (Fig. 105); widespread Central America to Argentina (Map 2) ..... *veniliae*

– Abdomen marked otherwise; posterior median plate otherwise 23

23(22). Posterior median plate round (Fig. 606); southwestern Colombia (Map 5) ..... *silencio*

– Posterior median plate otherwise 24

24(23). Median lobe triangular, with sides of epigynum rounded (Fig. 122); posterior median plate (Fig. 123); Amazon area to Argentina (Map 2) ..... *carminea*

– Epigynum otherwise 25

25(24). Posterior edge of epigynum on each side of lobe concave (Fig. 154); posterior median plate tripartite (Fig. 155); abdomen oval (Fig. 156); Bolivia to southern Brazil and Argentina (Map 3) ..... *versicolor*

– Posterior edge otherwise (Figs. 191, 194, 198); posterior median plate otherwise (Figs. 192, 195); abdomen elongate (Fig. 197) or widest posteriorly (Figs. 193, 200) 26

26(25). Posterior median plate narrowing dorsally (Fig. 192); northern Colombia (Map 3) ..... *kochalkai*

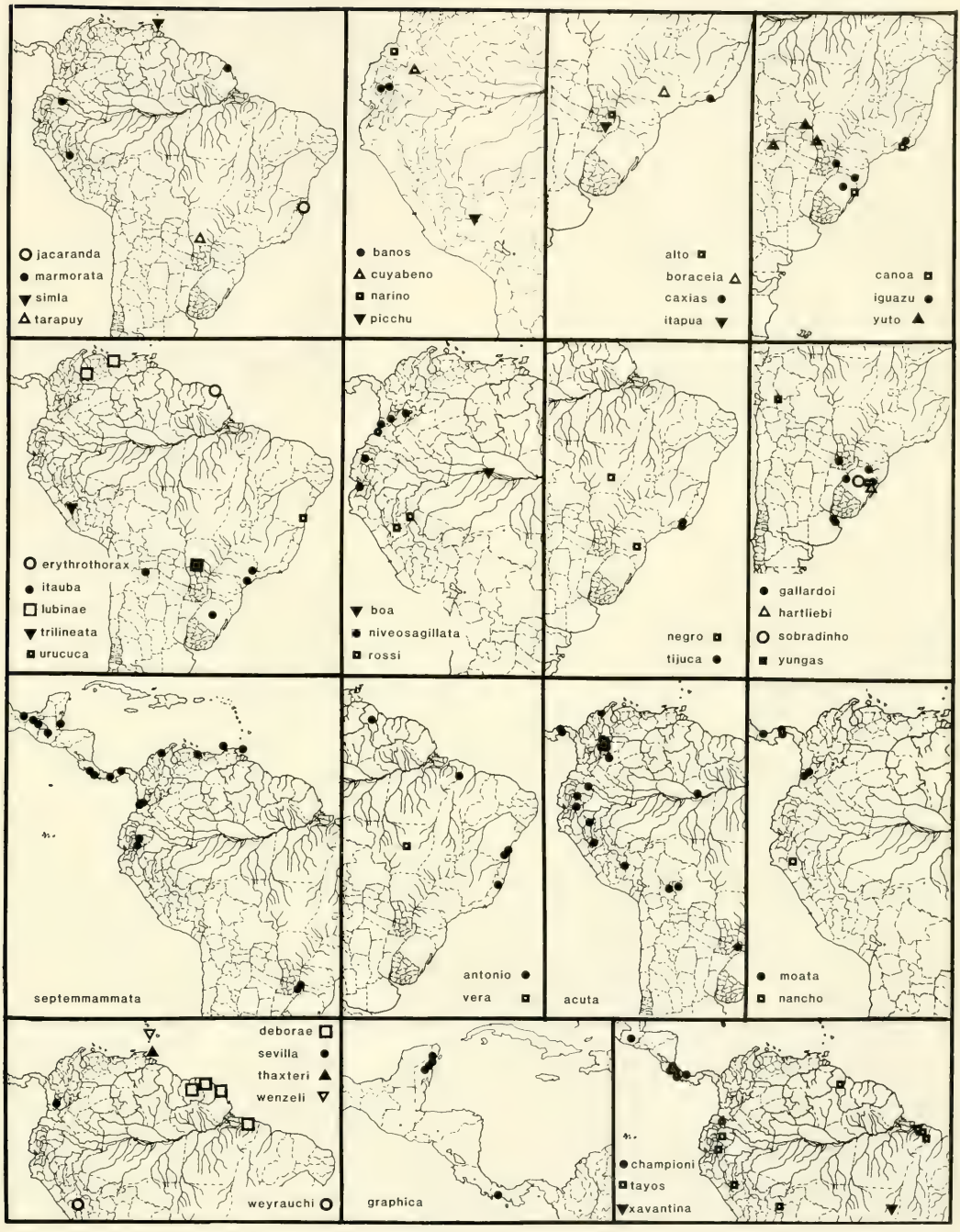
– Posterior median plate otherwise (Figs. 195, 199) 27

27(26). Epigynum in posterior view about as wide as long (Fig. 199); central Colombia (Map 3) ..... *variablis*

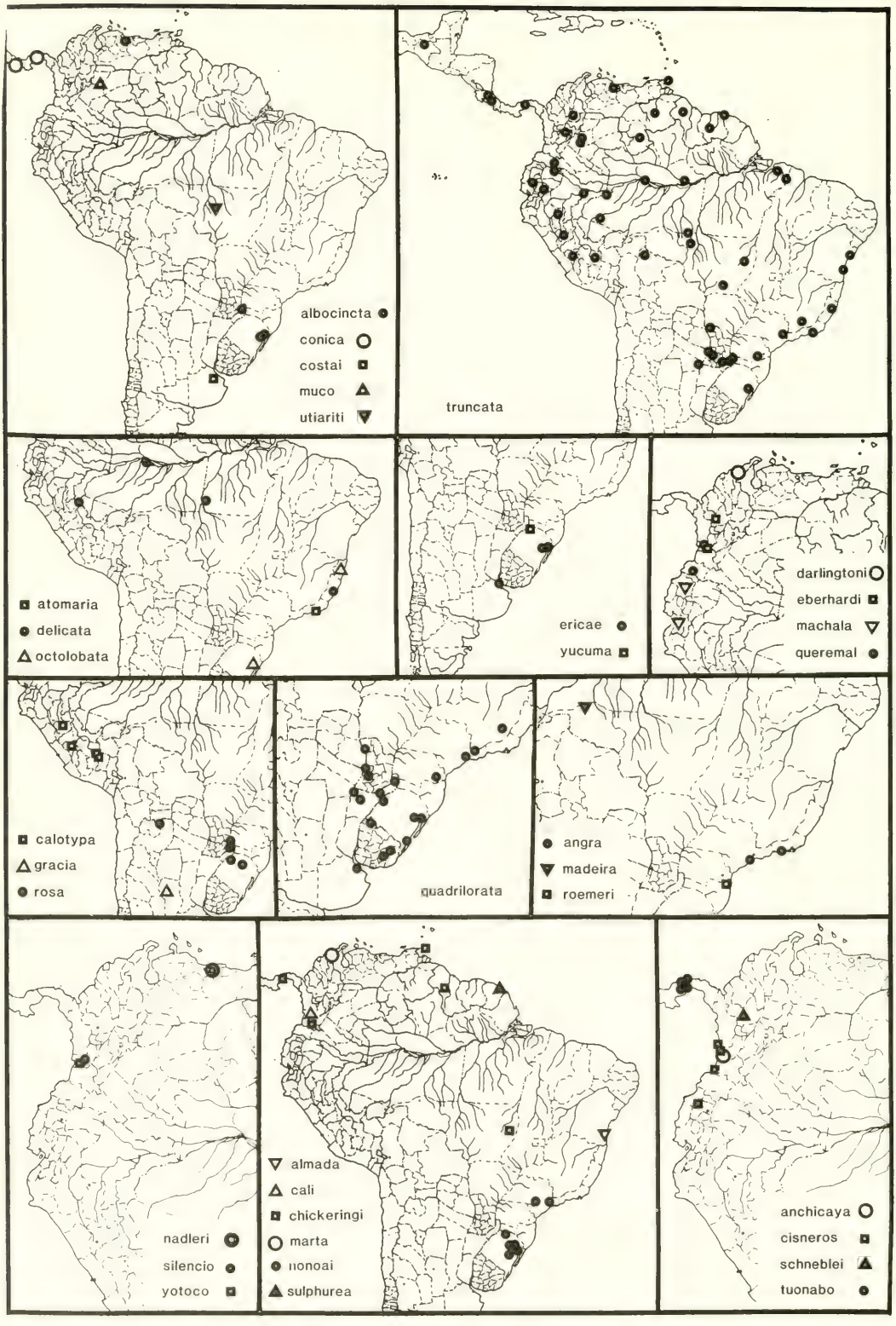
– Epigynum in posterior view longer than wide (Fig. 195); Amazon drainage (Map 3) ..... *iquitos*

28(14). Posterior margin of median notch anterior to posterior edge of epigynum (Figs. 44, 376, 381, 392) 29

– Epigynum without notch, or if with



Map 4. Distribution of *Alpaida* species.



Map 5. Distribution of *Alpaida* species.

median notch, its posterior margin is in line with margin of epigynum or posterior to it (Figs. 110, 147) 44

29(28). Abdomen all black with a pair of sclerotized tubercles (Fig. 437); Yucatan Peninsula to Panama (Map 4) ..... *graphica*

– Abdomen otherwise 30

30(29). Epigynum without median lobe (Fig. 172); posterior median plate as in Figure 173 and abdomen narrow (Fig. 174); Misiones Prov., Argentina (Map 3) ..... *montecarlo*

– If abdomen narrow, epigynum otherwise 31

31(30). Abdomen with median white longitudinal band, or white dorsally (Figs. 46, 88, 130, 463) 32

– Abdomen marked otherwise (Figs. 442, 454) 39

32(31). Notch the distance of its width or more from posterior margin (Figs. 44, 460, 468) 33

– Notch closer to posterior margin (Figs. 57, 86, 128, 166) 36

33(32). Epigynum triangular in posterior view (Fig. 447); venter of abdomen black (Fig. 449); Guatemala to Panama (Map 4) ..... *championi*

– Epigynum otherwise; venter not all black 34

34(33). Epigynum rectangular (Figs. 458, 460); Amazon area (Map 4) ..... *tayos*

– Outline of epigynum a semicircle or oval (Figs. 44, 468) 35

35(34). Median lobe longer than wide, with posterior edge notched on each side of lobe (Fig. 44); southeastern Brazil, Misiones Prov., Argentina (Map 2) ..... *grayi*

– Median lobe as wide as long (Fig. 468); northern Peru (Map 4) ..... *nancho*

36(32). Abdomen posteriorly constricted (Fig. 88); postertior median plate narrow ventrally (Fig. 87); Mato Grosso, Brazil (Map 2) ..... *cuiaba*

– Abdomen and posterior median plate otherwise 37

37(36). Posterior median plate almost rectangular with narrow lip framing plate (Fig. 129); lower Amazon to Mato Grosso (Map 2) ..... *alvarengai*

– Posterior median plate otherwise (Figs. 58, 167) 38

38(37). Notch of epigynum wider than long (Fig. 57); posterior median plate almost triangular (Fig. 58); southern Brazil to Argentina (Map 2) ..... *rubellula*

– Notch of epigynum as wide as long (Fig. 166); posterior median plate wider ventrally than dorsally (Fig. 167); Goiás, Brazil (Map 3) ..... *morro*

39(31). Notch of epigynum much wider than long (Fig. 381); central Peru (Map 4) ..... *trilineata*

– Notch of epigynum about as wide as long (Figs. 376, 386) 40

40(39). Notch its width or less from posterior edge (Figs. 392, 440) 41

– Notch more than its width from posterior edge (Figs. 376, 386, 452) 42

41(40). In posterior view, lip widest ventrally (Fig. 441); Bahia, Brazil (Map 4) ..... *urucuca*

– In posterior view, lip as wide dorsally as ventrally (Fig. 393); Guyana to eastern Brazil (Map 4) ..... *antonio*

42(40). Posterior median plate semicircular with 3 dorsal notches (Fig. 453); eastern Amazon area (Map 4) ..... *xavantina*

– Posterior median plate otherwise (Figs. 377, 387) 43

43(42). Sides of epigynum strongly curved (Fig. 386); Bolivia to southern Brazil (Map 4) ..... *itauba*

– Sides of epigynum less curved (Fig. 376); French Guiana (Map 4) ..... *erythrothorax*

44(28). Abdomen truncate posteriorly with 4 posterior humps, each covered by a black patch (Fig. 574); widespread from southern Mexico to northern Argentina (Map 5) ..... *truncata*

– Abdomen otherwise 45

45(44). Epigynum without notch or lip (Figs. 19, 50, 579) 46

– Epigynum with lip, notch or median groove (Figs. 110, 519, 530, 537) 54

46(45). Abdomen with 3 lateral lobes (Fig. 485); posterior median plate almost square (Fig. 484); southeastern Brazil (Map 5) ..... *octolobata*

– Abdomen, posterior plate otherwise 47

47(46). Epigynum with median anterior edge (Figs. 555, 564) 48

– Epigynum without median anterior edge (Figs. 19, 559, 579) 49

48(47). In posterior view, lips with ventral arms (Fig. 555); Colombia (Map 5) ..... *eberhardi*

– In posterior view, lips extend ventrally and laterally (Fig. 565); southwestern Colombia (Map 5) ..... *queremal*

49(47). Epigynum with anterior stalk (Figs. 559, 561); western Ecuador (Map 5) ..... *machala*

– Epigynum otherwise 50

50(49). Epigynum with a lobe on each side (Figs. 19, 20); Guyana to Mato Gros-

so and Bahia, Brazil (Map 2) ..... *guimaraes*
– Epigynum otherwise 51
51(50). Epigynum triangular (Figs. 551, 552); southern Brazil (Map 5) ..... *roemeri*
– Epigynum otherwise 52
52(51). Posterior median plate hardly wider than lips on each side (Fig. 580); southwestern Colombia (Map 5) ..... *yotoco*
– Posterior median plate much wider than lips (Figs. 53, 584) 53
53(52). Abdomen with a median anterior hump (Fig. 54); epigynum with a pointed scape (Fig. 50); posterior median plate oval (Fig. 53); southern Brazil (Map 2) ..... *rostratula*
– Abdomen without anterior hump (Fig. 585); epigynum with rounded lobe (Fig. 583); posterior median plate divided by lips dorsally into 2 lobes (Fig. 584); Venezuela (Map 5) ..... *nadleri*
54(45). Lobe of epigynum pointed, with a slight proximal constriction (Fig. 300); southern Brazil, northern Argentina (Map 4) ..... *gallardoi*
– Lobe never with constriction 55
55(54). Posterior median plate longer than wide (Figs. 26, 199, 365, 473) 56
– Posterior median plate wider than long 59
56(55). Lips with lobe on each side in posterior view (Fig. 26); abdomen with bands (Fig. 27); Peruvian Amazon drainage (Map 2) ..... *utcuyacu*
– Lips without lobes 57
57(56). Sides of median plate convex (Fig. 473); epigynum as Figure 472; Amazon area to eastern Brazil (Map 5) ..... *delicata*
– Sides of median plate parallel (Figs. 199, 365) 58
58(57). Epigynum with lip recurved, the middle of lip most anterior (Fig. 364); Guianas, lower Amazon (Map 4) ..... *deborae*
– Epigynum with lip procurved (Fig. 198); west central Colombia (Map 3) ..... *variabilis*
59(55). Posterior median plate partially divided in middle by swollen lip (Figs. 331, 337) 60
– Posterior median plate not so divided 61
60(59). Median swellings of lips (in posterior view) much longer than wide (Fig. 331); southern Brazil, Misiones Prov., Argentina (Map 4) ..... *iguazu*
– Median swellings of lips barely longer than wide (Fig. 337); southeastern Brazil (Map 4) ..... *tijuca*
61(59). Lips of epigynum folded and projecting anteriorly (Figs. 280–283, 285); Amazon area (Map 4) ..... *marmorata*
– Lips otherwise 62
62(61). Lips with anterior margin transverse (Figs. 140, 294, 360, 367) 63
– Lips otherwise 67
63(62). Abdomen black with median ventral white patch (Figs. 423, 424); epigynum as in Figures 421, 422; Panama to northern Argentina (Map 4) ..... *acuta*
– Abdomen and epigynum otherwise 64
64(63). Abdomen banded (Fig. 142); epigynum as in Figures 140, 141; northern Paraguay (Map 2) ..... *chaco*
– Abdomen and epigynum otherwise 65
65(64). Median lobe set off, with parallel sides (Fig. 367); Venezuela (Map 4) *lubinae*
– Median lobe triangular 66
66(65). Only median lobe triangular (Fig. 294); southeastern Brazil (Map 4) ..... *hartliebi*
– Median lobe and lips forming a triangle (Fig. 360); Peru (Map 4) ..... *weyrauchi*
67(62). Median lobe rounded and slightly constricted at base (Fig. 404); Amazonian Peru (Map 4) ..... *rossi*
– Median lobe otherwise 68
68(67). Abdomen barely longer than wide, with humps as in Figures 481, 482; epigynum as in Figure 479; Rio de Janeiro, Brazil (Map 5) ..... *atomaria*
– Abdomen and epigynum otherwise 69
69(68). Posterior end of abdomen truncate with side of posterior end parallel and slightly constricted at base (Figs. 549, 550); western Brazil (Map 5) ..... *madeira*
– Abdomen otherwise 70
70(69). Abdomen with white semicircular marks around side enclosing dark mark (Figs. 177, 179); epigynum as in Figure 175; central to southeastern Brazil, Paraguay (Map 3) ..... *latro*
– Abdomen and epigynum otherwise 71
71(70). Abdomen oval, contrastingly marked with bands or paired patches as in Figues 532, 533, 539; epigynum with anterior edge of lip indistinct (Figs. 530, 537) 72
– Abdomen or epigynum otherwise 73
72(71). Abdomen with black median band (Fig. 539); southeastern Brazil (Map 5) ..... *angra*
– Abdomen always with white to orange median band (Figs. 532, 533); southeastern Brazil, Paraguay to northern Argentina (Map 5) ..... *quadrilorata*
73(71). Abdomen subspherical, light, or dark with light marks (Figs. 230, 233) 74
– Abdomen otherwise 75

74(73). Abdomen dark with light marks (Fig. 233); epigynum as in Figure 231; southeastern Brazil (Map 3) ..... *biasii*
– Abdomen light colored (Fig. 230); epigynum with dark line on lip (Fig. 228); Mato Grosso, Brazil (Map 3) ..... *mato*
75(73). Abdomen distinctly marked as in Figure 41; Bolivia (Map 2) ..... *coroico*
– Abdomen otherwise 76
76(75). Abdomen with 3 light bands on dorsum (Figs. 35, 99, 136) 77
– Abdomen otherwise 79
77(76). Epigynum semicircular on each side of median lobe (Fig. 32); widespread, Panama to Argentina (Map 2) ..... *leucogramma*
– Epigynum otherwise 78
78(77). Epigynum with median lobe set off (Fig. 97); Mato Grosso to lower Amazon, Brazil (Map 2) ..... *chapada*
– Epigynum with median lobe forming a triangle with lips, not set off (Fig. 134); Argentina (Map 2) ..... *holmbergi*
79(76). Abdomen shield-shaped with paired patches (Fig. 112); venter with triangular light spot (Fig. 113); epigynum as in Figures 110, 111; widespread, Amazon area to eastern Brazil (Map 3) ..... *tabula*
– Abdomen and epigynum otherwise 80
80(79). Abdomen with grooves on sides (Fig. 527); epigynum with posterior median plate swollen on each side (Fig. 526); Venezuela, southern Brazil (Map 5) ..... *albocincta*
– Abdomen or epigynum otherwise 81
81(80). Abdomen black oval with white lines (Figs. 521, 522); epigynum hexagonal, with sides almost parallel (Fig. 519); eastern Colombia (Map 5) ..... *muco*
– Abdomen and epigynum otherwise 82
82(81). Abdomen with 6 round patches (Fig. 221); southeastern Brazil (Map 3) ..... *lomba*
– Abdomen marked otherwise 83
83(82). Abdomen subspherical, dark with white shoulder marks and venter light (Figs. 118, 119); anterior edge of lip concave (Fig. 116); southeastern Brazil, northern Argentina (Map 2) ..... *rioja*
– Abdomen and epigynum otherwise 84
84(83). Abdomen with 3 anterior tubercles and scalloped dorsal markings (Fig. 94) and epigynum as in Figure 92, median plate with 2 dark marks dorsally (Fig. 93); southeastern Brazil, Paraguay (Map 2) ..... *hoffmanni*
– Abdomen and epigynum otherwise 85
85(84). Posterior plate with a median dorsoventral raised plate with parallel sides (Fig. 144); Lesser Antilles (Map 2) ..... *elegantula*
– Posterior median plate otherwise 86
86(85). Abdomen with a "tail" beyond spinnerets (Figs. 508, 509, 514) 87
– Abdomen without tail, rounded or pointed behind 88
87(86). Median lobe of epigynum almost in line with sides (Fig. 506); posterior median plate oval (Fig. 507); Panama (Map 5) ..... *conica*
– Median lobe extending posteriorly beyond sides (Fig. 512); posterior plate with 2 lobes (Fig. 513); northern Argentina (Map 5) ..... *gracia*
88(86). Abdomen with paired black marks, hairy humps on sides and posterior hairy hump (Figs. 184, 185); epigynum with polished V-shaped lip (Fig. 182); southeastern Brazil (Map 3) ..... *alticeps*
– Abdomen otherwise 89
89(88). Abdomen more than twice as long as wide (Figs. 151, 162, 190, 613, 625) 90
– Abdomen oval, shorter 93
90(89). Median lobe semicircular, lips indistinct (Figs. 160, 161); Peruvian Amazon area to southeastern Brazil, Misiones Prov., Argentina (Map 2) ..... *vanzolinii*
– Epigynum otherwise 91
91(90). Epigynum with semicircular notch (Fig. 611); abdomen with black spots (Figs. 613, 614); southern Colombia (Map 5) ..... *cali*
– Epigynum and abdomen otherwise 92
92(91). Lips of epigynum polished, V-shaped (Fig. 188); posterior median plate oval (Fig. 189); Espírito Santo, Brazil (Map 3) ..... *scriba*
– Notch on end of median lobe (Fig. 623); posterior median plate with 2 lobes (Fig. 624); northern Colombia (Map 5) ..... *marta*
93(89). Abdomen only slightly longer than wide, shield-shaped, with white pigment all around sides (Fig. 218); epigynum as in Figures 216, 217; southeastern Brazil (Map 3) ..... *canela*
– Abdomen and epigynum otherwise 94
94(93). Abdomen with humps all around dorsally (Figs. 429, 488, 489, 493) 95
– Abdomen usually entire, sometimes with an anterior tubercle and sometimes pointed behind 97
95(94). Abdomen mostly black and gray with 2 ventral white spots (Figs. 429, 431); southern Mexico, Colombia, Venezuela, northern Argentina (Map 4) ..... *septemmammata*

– Abdomen light colored 96
96(95). Median lobe of epigynum pointed and larger than sides (Fig. 486); southeastern Brazil, northern Argentina (Map 5) ..... *ericae*
– Median lobe rounded and small (Fig. 491); southeastern Brazil (Map 5) ..... *yucuma*
97(94). Abdomen with cardiac area black, in contrast to adjacent light orange shoulder areas (Fig. 308); epigynum as in Figures 306, 307; southeastern Brazil (Map 4) ..... *sobradinho*
– Abdomen of various coloration but cardiac area usually with white pigment spots; epigynum otherwise 98
98(97). Abdomen with median dorsal white band, sometimes broken, with patches of black and white on sides (Figs. 241, 245, 249, 255, 497, 619) 99
– Abdomen mostly light (Figs. 151, 206, 209, 225, 236, 503) or abdomen mostly black and gray with a white cardiac mark (Figs. 259, 315, 417, 442) 104
99(98). Posterior median plate visible in ventral view of epigynum, surrounded by a lip on each side of the median lobe (Figs. 495, 617) 100
– Posterior median plate barely visible in ventral view (Figs. 239, 243) 101
100(99). Median lobe V-shaped (Fig. 617); southeastern Brazil (Map 5) ..... *nonoai*
– Median lobe U-shaped with parallel sides (Fig. 495); southeastern Brazil to Bolivia (Map 5) ..... *rosa*
101(99). Posterior median plate with 2 dorsal notches (Fig. 240); Rio de Janeiro, Brazil (Map 3) ..... *orgaos*
– Posterior median plate entire (Fig. 244, 247, 254) 102
102(101). Median lobe with notch (Figs. 246, 248); posterior median plate with 2 dorsal dark marks (Fig. 247); southeastern Brazil (Map 3) ..... *pedro*
– Notch more anterior (Figs. 243, 253); posterior median plate without dark marks (Figs. 244, 254) 103
103(102). Median lobe a minute tubercle (Fig. 253); posterior median plate subtriangular (Fig. 254); Bolivia (Map 3) ..... *moka*
– Median lobe rounded large (Fig. 243); posterior median plate oval (Fig. 244); Rio de Janeiro, Brazil (Map 3) ..... *sumare*
104(98). Abdomen mostly light (Figs. 151, 206, 209, 225, 236, 503) 105
– Abdomen mostly black and gray with a white cardiac mark (Figs. 259, 315, 417, 442) 110
105(104). Median lobe with a groove (Figs. 223, 224, 234, 235) 106
– Median lobe with a V- or U-shaped notch, or without a notch or groove (Figs. 147, 204, 207, 501) 107
106(105). Lips entire with a dark anterior border (Fig. 223); abdomen with grooves on sides (Fig. 225); southeastern Brazil (Map 3) ..... *nigrofrenata*
– Lips with anterior margin broken (Fig. 234); abdomen without grooves on sides (Fig. 236); São Paulo, Brazil (Map 3) ..... *bischoffi*
107(105). Posterior median plate visible as a bulge on each side of median lobe; lobe with a deep notch (Fig. 501); Peru (Map 5) ..... *calotypa*
– Posterior median plate barely visible in ventral view (Figs. 147, 204, 207) 108
108(107). Abdomen with an anterior median tubercle (Figs. 206, 209) 109
– Abdomen without such a tubercle (Fig. 151); Lesser Antilles (Map 2) ..... *dominica*
109(108). Median lobe pointed (Fig. 207); dorsally posterior median plate with 2 sclerotized teeth (Fig. 208); southeastern Brazil (Map 3) ..... *sandrei*
– Median lobe rounded (Fig. 204); posterior median plate with 2 slightly sclerotized bulges dorsally facing median (Fig. 205); southeastern Brazil (Map 3) ..... *citrina*
110(104). Median lobe of epigynum a pointed triangle, not bordered toward posterior median plate (Figs. 257, 342) 111
– Median lobe always discrete (Figs. 348, 398) 112
111(110). Posterior median plate rectangular (Fig. 258); Venezuela (Map 3) ..... *haligera*
– Posterior median plate oval (Fig. 343); St. Vincent Island, Lesser Antilles (Map 4) ..... *wenzeli*
112(110). Length of posterior median plate visible on each side of median lobe equal or greater than thickness of lips (Figs. 348, 398) 113
– Posterior median plate barely visible on each side of median lobe (Figs. 354, 440) 115
113(112). Median lobe V-shaped (Figs. 317, 348) 114
– Median lobe U-shaped with parallel sides and thin lips (Fig. 398); Colombia, Ecuador (Map 4) ..... *niveosagillata*
114(113). Lips thick (Fig. 348); posterior median plate angular (Fig. 349); southeastern Brazil (Map 4) ..... *canoa*

– Lips otherwise (Fig. 317); posterior median plate three-partite, ends rounded (Fig. 318); southern Colombia (Map 4) ..... *sevilla*

115(112). Width of median lobe wider than areas on each side (Fig. 289); Trinidad (Map 4) ..... *simla*

– Width of median lobe narrower than area on each side. 116

116(115). Width of median lobe much greater than thickness of indistinct lips on each side (Figs. 410, 415) 117

– Width of median lobe equal or narrower than thickest part of lips (Figs. 324, 354, 440) 118

117(116). Posterior median plate with a transverse groove (Fig. 411); Mato Grosso, southeastern Brazil (Map 4) ... *negro*

– Posterior median plate with dorsoventral ridge (Fig. 416); Panama, Colombia (Map 4) ..... *moata*

118(116). Lips with margins parallel (Figs. 310, 313, 324) 119

– Lips swollen, margins bulging (Figs. 320, 354, 427, 440) 121

119(118). Width of posterior median plate about 1.6 times dorsoventral length, plate constricted in middle (Fig. 314); Amazonian Peru (Map 4) ..... *picchu*

– Width of posterior median plate about twice dorsoventral length, plate not constricted in middle (Figs. 311, 325) 120

120(119). Posterior median plate angular (Fig. 325); Trinidad (Map 4) ..... *thaxteri*

– Posterior median plate rounded on sides (Fig. 311); southeastern Brazil, Bolivia (Map 4) ..... *itapua*

121(118). Poterior median plate with sides straight, plate wider ventrally than dorsally (Fig. 355); Paraguay, northern Argentina (Map 4) ..... *yuto*

– Posterior median plate otherwise (Figs. 321, 428, 441) 122

122(121). Lips of posterior median plates bulging on sides ventrally (Fig. 441); Bahia, Brazil (Map 4) ..... *urucuca*

– Lips of about equal width around posterior median plate (Figs. 321, 428) 123

123(122). Dorsal border of posterior median plate overhung by a pair of tubercles (Fig. 428); venter of abdomen with a pair of white patches (Fig. 431); southern Mexico, Venezuela, Colombia, northern Argentina (Map 4) ..... *septemmammata*

– Dorsal border of posterior median plate bordered by slightly swollen lips (Fig. 321); venter of abdomen with a pair of white lines (Fig. 323); Paraguay (Map 4) ..... *alto*

KEY TO MALES

Terms used in the key are illustrated by Figures 6 and 10. Descriptions of palpus are all of the left palpus in mesal view with the cymbium at the left, as are all illustrations.

1. Palpal tibia as long as cymbium or longer (Fig. 477); first coxa without hook, second femur without groove; Amazon area to southeastern Brazil (Map 5) ..... *delicata*

– Palpal tibia much shorter than cymbium (Figs. 18, 30, 43); first coxa always with hook and second femur with groove (Fig. 6) 2

2(1). Palpal patella with 2 equal-sized, long setae 3

– Palpal patella with only 1 long seta (Fig. 6) 5

3(2). Median apophysis long, wider distally than proximally, tegulum with a tubercle at edge, terminal apophysis rectangular (Fig. 252); southeastern Brazil (Map 3) ..... *pedro*

– Median apophysis not long and not noticeably wider distally; tegulum entire, terminal apophysis distally bent lobe (Figs. 634, 639) 4

4(3). Terminal apophysis with tip of distal lobe projecting away from tegulum (Fig. 634); Panama, Guianas to Colombia (Map 5) ..... *chickeringi*

– Terminal apophysis with tip of distal lobe pointing toward tegulum (Fig. 639); Bahia, Brazil (Map 5). ..... *almada*

5(2). Abdomen with 3 anterior spines (Figs. 73, 78) 6

– Abdomen with at most a median anterior tubercle 7

6(5). Median apophysis longer than wide; terminal apophysis a bent flat rod (Fig. 74); southeastern Brazil (Map 2) ..... *keyserlingi*

– Median apophysis as long as wide; terminal apophysis with sides bulging (Fig. 79); northern Peru (Map 2) ..... *monzon*

7(5). Median apophysis distally drawn beyond tegulum, bent around tegulum (Figs. 569, 577) or projecting (Fig. 592) 8

– Median apophysis otherwise 10

8(7). Second tibiae flattened (Fig. 578); abdomen with 4 posterior tubercles (Fig. 576); widespread, southern Mexico to Argentina (Map 5) ..... *truncata*

– Second tibiae not so modified; abdomen rounded behind (Figs. 568, 591) 9

9(8). Embolus filiform; median apophysis projecting away from tegulum (Fig. 592); southern Colombia (Map 5) ..... *anchicaya*

– Embolus short; median apophysis curved parallel to edge of tegulum (Fig. 569); southern Colombia (Map 5) ..... *queremal*

10(7). Tegulum with "shutters" under terminal apophysis (Fig. 109); widespread, Panama to Argentina (Map 2) ..... *veniliae*
– Tegulum without "shutters" 11
11(10). Embolus or its end coiled or filamentous (Figs. 68, 91, 121, 133, 181, 546, 604) 12
– Embolus otherwise 23
12(11). Abdomen with light patches enclosing darker marks around edge (Fig. 180); palpus as in Figure 181; Amazon to southeastern Brazil (Map 3) ..... *latro*
– Abdomen and palpus otherwise 13
13(12). Abdomen banded and with anterior median tubercle (Fig. 67); palpus with large thorn on median apophysis (Fig. 68); widespread, Panama to northern Argentina (Map 2) ..... *trispinosa*
– Abdomen and palpus otherwise 14
14(13). Embolus U-shaped in ventral view (Fig. 91); Mato Grosso, Brazil (Map 2) ..... *cachimbo*
– Embolus otherwise 15
15(14). Base of embolus visible from side of palpus, originating from underneath cymbium (Figs. 121, 133, 409) 16
– Base of embolus originating from "top" of bulb (Figs. 546, 604, 610, 616, 622, 627) 18
16(15). Terminal apophysis with distal lobe pointing to tip of cymbium (Fig. 133); Pará to Mato Grosso, Brazil (Map 2) ..... *alvarengai*
– Terminal apophysis otherwise (Figs. 121, 409) 17
17(16). Terminal apophysis with distal lobe subtriangular, pointed (Fig. 121); southeastern Brazil, Argentina (Map 2) ..... *rioja*
– Terminal apophysis as in Figure 409; Amazonas, Brazil (Map 4) ..... *boa*
18(15). Embolus supported by conductor in distal half of bulb (Figs. 610, 616, 622) 19
– Embolus tip supported by conductor in middle or basal half of bulb (Figs. 546, 604, 627) 21
19(18). Median apophysis with a distal extension (Fig. 610); southern Colombia (Map 5) ..... *silencio*
– Median apophysis otherwise (Figs. 616, 622) 20
20(19). Embolus on top of bulb curled toward cymbium (Fig. 616); southern Colombia (Map 5) ..... *cali*
– Embolus curved toward base (Fig. 622); southeastern Brazil (Map 5) ..... *nonoai*
21(18). Median apophysis short, with a tooth (Fig. 627); northern Colombia (Map 5) ..... *marta*
– Median apophysis otherwise 22
22(21). Median apophysis long, pointed at each end (Fig. 546); northern Colombia (Map 5) ..... *darlingtoni*
– Median apophysis with blunt tooth in middle (Fig. 604); Colombia (Map 5) ..... *schneblei*
23(11). Embolus straight with parallel sides (Fig. 598); Panama (Map 5) ..... *tuonabo*
– Embolus otherwise 24
24(23). Embolus a slightly curved rod across the middle of palpus (Figs. 127, 524) 25
– Embolus otherwise 26
25(24). Distal lobe of terminal apophysis pointing back toward cymbium (Fig. 127); Amazon area to Argentina (Map 2) ..... *carminea*
– Distal lobe of terminal apophysis projecting (Fig. 524); Mato Grosso, Brazil (Map 5) ..... *utiariti*
26(24). Distal lobe of terminal apophysis with an arm and two projections (Figs. 153, 159, 500) 27
– Distal lobe of terminal apophysis otherwise 29
27(26). Median apophysis with distal lobe pointing toward terminal apophysis; edge of tegulum with point (Fig. 159); Bolivia, southeastern Brazil to Argentina (Map 3) ..... *versicolor*
– Median apophysis without such a lobe, visible portion of tegulum entire (Figs. 153, 500) 28
28(27). Median apophysis with a proximal tooth; basal prong of terminal apophysis wide (Fig. 500); southeastern Brazil, Misiones Prov., Argentina (Map 5) ..... *rosa*
– Median apophysis with a large median tooth; basal prong of terminal apophysis narrow (Fig. 153); Lesser Antilles (Map 2) ..... *dominica*
29(26). Distal lobe and basal prong of terminal apophysis alike in shape and one slightly "below" other (Fig. 505); Peru (Map 5) ..... *calotypa*
– Distal lobe and basal prong unlike each other (Figs. 115, 426, 536) 30
30(29). Abdomen shield-shaped with paired spots (Fig. 114); palpus as in Figure 115; Venezuela, Ecuador to Mato Grosso, and Bahia, Brazil (Map 3) ..... *tabula*
– Abdomen and palpus otherwise 31
31(30). Abdomen with sclerotized disks (Figs. 425, 535); palpus as in Figures 426 or 536 32
– Abdomen lacking sclerotized disks 33
32(31). Abdomen black (Fig. 425); terminal apophysis of palpus with distal lobe bent on itself, basal prong straight

(Fig. 426); Panama to Misiones Prov., Argentina (Map 4) ..... *acuta*

– Abdomen with black marks along dorsal border (Fig. 535); palpus with basal prong of terminal apophysis and embolus bent toward each other (Fig. 536); southeastern Brazil, Paraguay, northern Argentina (Map 5) ..... *quadrilorata*

33(31). Abdomen with a median anterior tubercle or spine (Figs. 214, 328); palpus as in Figure 215 or 329 34

– Abdomen rounded in front 35

34(33). Body with dark pigment (Fig. 328); median apophysis with a long proximal lobe (Fig. 329); Est. São Paulo, Brazil (Map 4) ..... *boraceia*

– Body without dark pigment (Fig. 214); median apophysis without proximal lobe (Fig. 215); Lower Amazon (Map 3) ..... *manicata*

35(33). Abdomen with a pair of slightly sclerotized shoulder tubercles (Fig. 438); palpus as in Figure 439; Yucatan to Panama (Map 4) ..... *graphica*

– Abdomen without such shoulder tubercles; palpus otherwise 36

36(35). Abdomen with 2 pairs of hairy lateral humps (Fig. 186); palpus with large circular terminal apophysis and median apophysis pointed at each end (Fig. 187); southeastern Brazil (Map 3) ..... *alticeps*

– Abdomen and palpus otherwise 37

37(36). Abdomen with longitudinal bands (Figs. 23, 48, 84, 450) 38

– Abdomen marked otherwise 48

38(37). Edge of tegulum evenly rounded (Figs. 24, 30, 62, 165, 451) 39

– Edge of tegulum with a flat lobe (Figs. 43, 85) or a pointed lobe (Figs. 38, 49, 56) 43

39(38). Distal lobe of terminal apophysis projecting from bulb and median apophysis projecting in opposite direction (Fig. 24); Guyana to Mato Grosso and Bahia, Brazil (Map 2) ..... *guimaraes*

– Terminal apophysis or median apophysis otherwise 40

40(39). Distal lobe of terminal apophysis projecting (Figs. 62, 451) 41

– Distal lobe of terminal apophysis bent toward conductor (Fig. 30) or only slightly extended (Fig. 165) 42

41(40). Median apophysis with a set-off distal extension (Fig. 451); Guatemala to Colombia (Map 4) ..... *championi*

– Median apophysis semicircular in ventral view with median tooth (Fig. 62); Mato Grosso, Brazil to northern Argentina (Map 2) ..... *rubellula*

42(40). Abdomen with almost parallel sides (Fig. 164); terminal apophysis distally tripartite; median apophysis with a blunt basal tooth (Fig. 165); western Amazon to southeastern Brazil (Map 3) ..... *vanzolinii*

– Abdomen oval (Fig. 29); terminal apophysis small, not divided distally; median apophysis with a median and proximal tooth (Fig. 30); Peru (Map 2) ..... *utcuyacu*

43(38). Edge of tegulum with a rounded lobe (Figs. 43, 85) 44

– Edge of tegulum with a pointed lobe (Figs. 38, 49, 56) 45

44(43). Terminal apophysis with row of denticles distally (Fig. 85); western Brazil (Map 2) ..... *murtinho*

– Terminal apophysis with a distally pointed triangular piece (Fig. 43); Bolivia (Map 2) ..... *coroico*

45(43). Terminal apophysis with a projecting lobe; median apophysis very long and pointed at each end; embolus hidden by terminal apophysis (Fig. 38); widespread, Panama to Argentina (Map 2) ..... *leucogramma*

– Terminal apophysis and median apophysis otherwise; embolus visible (Figs. 49, 56) 46

46(45). Distal lobe of terminal apophysis bent on itself, median apophysis with a keel and edge of tegulum drawn out to a point (Fig. 49); southeastern Brazil (Map 2) ..... *grayi*

– Terminal apophysis with 2 points, median apophysis a large flat sclerite, edge of tegulum bent forward (Figs. 18, 56) 47

47(46). Terminal apophysis with 2 tips at right angles; median apophysis subrectangular (Fig. 18); widespread Central America to Argentina (Map 2) ..... *bicornuta*

– Terminal apophysis with 2 tips facing same direction; median apophysis as in Figure 56; southeastern Brazil (Map 2) ..... *rostratula*

48(37). Abdomen with light round patches on dark background (Fig. 226) and median apophysis with a proximal projection (Fig. 227); eastern Brazil (Map 3) ..... *natal*

– Abdomen and median apophysis otherwise 49

49(48). Abdomen with lateral grooves around margin (Fig. 528); palpus with distal lobe and basal prong of terminal apophysis bent toward each other and

with short median apophysis (Fig. 529); Venezuela, southeastern Brazil (Map 5) ..... *albocincta*

– Palpus otherwise, abdomen entire 50

50(49). Bulb narrow; terminal apophysis with 2 tips at right angles and median apophysis subrectangular (Fig. 18); widespread, Central America to Argentina (Map 2) ..... *bicornuta*

– Bulb wider; terminal apophysis and median apophysis otherwise 51

51(50). Distal edge of terminal apophysis frayed as in Figures 380, 385 52

– Distal edge otherwise 53

52(51). Terminal apophysis with curved basal prong (Fig. 385); Peru (Map 4) ..... *trilineata*

– Terminal apophysis with 5 fingers and small basal prong distally (Fig. 380); Mato Grosso, Brazil (Map 4) ..... *vera*

53(51). Terminal apophysis with distinct distal lobe (Figs. 96, 102, 139, 203, 279, 375, 397) 54

– Terminal apophysis with distal margin entire or slightly notched, or folded in ventral view (Figs. 293, 341, 353, 391, 457, 467) 66

54(53). Distal lobe of terminal apophysis projecting and bent toward viewer or straight (Figs. 96, 139, 397, 420, 434, 445, 511) 55

– Distal lobe of terminal apophysis otherwise (Figs. 102, 203, 279, 375, 403, 414) 61

55(54). Distal lobe of terminal apophysis with tip bent (Figs. 96, 397, 434, 445) 56

– Distal lobe straight (Figs. 139, 511) 59

56(55). Median apophysis projecting beyond tegulum (Fig. 96); southeastern Brazil, Paraguay (Map 2) ..... *hoffmanni*

– Median apophysis small, framed by tegulum (Figs. 434, 445) 57

57(56). Basal prong large, distinct (Fig. 434); Veracruz, Mexico to Misiones Prov., Argentina (Map 4) ..... *septemmammata*

– Basal prong a minute point or absent 58

58(57). Edge of tegulum with a pointed tubercle half way between median and terminal apophysis; basal prong a minute point (Fig. 397); Guyana to southeastern Brazil (Map 4) ..... *antonio*

– Edge of tegulum with tubercle closer to median than to terminal apophysis; basal prong absent (Fig. 445); Bahia, Brazil (Map 4) ..... *urucuca*

59(55). Median apophysis flat (Fig. 139); Bahia, Brazil (Map 4) ..... *santosi*

– Median apophysis otherwise 60

60(59). Distal lobe of terminal apophysis with a finger; basal prong a small hook; axis of embolus parallels that of cymbium (Fig. 420); Panama, Colombia (Map 4) ..... *moata*

– Distal lobe without finger, basal prong large curved structure; axis of embolus at right angle to that of cymbium (Fig. 511); Panama (Map 5) ..... *conica*

61(54). Median apophysis with a convex lobe on "upper" surface (Fig. 102); Upper Amazon, Brazil (Map 2) ..... *constant*

– Median apophysis with "upper" surface concave, sometimes with tooth (Figs. 375, 403) 62

62(61). Median apophysis with median tooth (Figs. 203, 403) 63

– Median apophysis with proximal tooth (Figs. 279, 375, 414) 64

63(62). Edge of tegulum with a pointed tubercle (Fig. 403); southern Colombia, Ecuador (Map 4) ..... *niveosagillata*

– Edge of tegulum with a round lobe (Fig. 203); Colombia (Map 3) ..... *variabilis*

64(62). Edge of tegulum with a tubercle; terminal apophysis a hood over its distal lobe (Fig. 279); Lower Amazon area (Map 3) ..... *gurupi*

– Edge of tegulum without tubercle; terminal apophysis otherwise (Figs. 375, 414) 65

65(64). Terminal apophysis with curved prong and large transparent conductor equal in size to terminal apophysis; edge of tegulum not bent (Fig. 375); Bolivia (Map 4) ..... *yungas*

– Terminal apophysis with lobed prong and transparent conductor smaller than terminal apophysis; edge of tegulum twisted to side of median apophysis (Fig. 414); Mato Grosso, southeastern Brazil (Map 4) ..... *negro*

66(53). Median apophysis ovoid, "upper" margin convex (Fig. 299); Bahia, Brazil (Map 4) ..... *jacarunda*

– Median apophysis with "upper" margin concave or with 1 or 2 teeth 67

67(66). Median apophysis projecting beyond tegulum (Fig. 373); Venezuela (Map 4) ..... *lubinae*

– Median apophysis otherwise 68

68(67). Median apophysis with a distal fold bearing 2 blunt teeth (Fig. 391); southeastern Brazil (Map 4) ..... *itauba*

– Median apophysis without such a fold 69

69(68). Median apophysis with a median slender tooth (Fig. 359); Paraguay, northern Argentina (Map 4) ..... *yuto*

– Median apophysis without median tooth 70

70(69). Embolus a flat angular structure with lobes, subequal in size to terminal

apophysis (Fig. 293); Trinidad (Map 4) ..... *simla*

– Embolus with pointed tip always much smaller than terminal apophysis 71

71(70). Terminal apophysis with projecting rugose finger on margin toward cymbium (Fig. 341); Rio de Janeiro, Brazil (Map 4) ..... *tijuca*

– Terminal apophysis without such a finger 72

72(71). Terminal apophysis without basal prong or basal prong indistinct (Figs. 171, 238, 305) 73

– Terminal apophysis a distinct heavily sclerotized structure (Figs. 266, 335, 353) 75

73(72). Edge of tegulum entire; transparent conductor smaller than terminal apophysis (Fig. 238); São Paulo, Brazil (Map 3) ..... *bischoffi*

– Edge of tegulum with broad lobe; transparent conductor of equal size or larger than terminal apophysis (Figs. 171, 305) 74

74(73). Edge of tegulum with large lobe; "lower" margin of median apophysis strongly convex (Fig. 305); southeastern Brazil, Paraguay, Argentina (Map 4) ..... *gallardoi*

– Edge of tegulum with small lobe; "lower" margin of median apophysis only slightly convex (Fig. 171); southeastern Brazil (Map 3) ..... *lanei*

75(72). Edge of tegulum with pointed tubercle (Fig. 266); Ecuador (Map 4) ..... *banos*

– Edge of tegulum with lobe or rounded tubercle (Figs. 335, 347) 76

76(75). Diameter of basal prong equal to half diameter of terminal apophysis (Fig. 467); Ecuador, Peru (Map 4) ..... *tayos*

– Diameter of basal prong less than one-third of diameter of terminal apophysis 77

77(76). Terminal apophysis with median ridge paralleling basal prong (Fig. 353); southeastern Brazil (Map 4) ..... *canoa*

– Terminal apophysis otherwise 78

78(77). Basal prong hanging from "left" distal margin of terminal apophysis above cymbium (Fig. 335); southeastern Brazil, Misiones Prov., Argentina (Map 4) ..... *iguazu*

– Basal prong at proximal margin of terminal apophysis to "right" of cymbium (Figs. 347, 457) 79

79(78). Edge of tegulum with a broad lobe; median apophysis short with tooth near proximal end (Fig. 457); Lower Amazon to Mato Grosso, Brazil (Map 4) ..... *xavantina*

– Edge of tegulum with blunt tubercle; median apophysis long with tooth at proximal end (Fig. 347); Rio de Janeiro, Brazil (Map 4) ..... *caxias*

Alpaida bicornuta (Taczanowski), new combination

Plate 1; Figures 11–18; Map 2

Epeira bicornuta Taczanowski, 1878: 168, pl. 2, fig. 18, ♀. Female lectotype here designated, and paralectotypes from Pumamarca and Amable María, Junín, Peru (PAN), examined.

Epeira spinigera O. P.-Cambridge, 1889: 43, pl. 5, figs. 9, 10, ♀. Female holotype from Bugaba, Panama (BMNH), examined. Keyserling, 1892: 131, pl. 7, fig. 97, ♀. McCook, 1894: 191, pl. 14, figs. 3, 4. NEW SYNONYMY.

Aranea spinigera:—F. P.-Cambridge, 1904: 515, pl. 49, fig. 16, ♀. Roewer, 1942: 853. Bonnet, 1955: 602.

Araneus designatus Chamberlin and Ivie, 1936: 51, pl. 14, figs. 126, 127. Immature female from Barro Colorado Island, Panama, just before final molt (AMNH), examined. Roewer, 1942: 841. Bonnet, 1955: 486. NEW SYNONYMY.

Aranea bicornuta:—Roewer, 1942: 837.

Wixia fissifasciata Mello-Leitão, 1945: 244, fig. 27, ♀. Female holotype from Pindapoy, Prov. Misiones, Argentina (MLP), examined. NEW SYNONYMY.

Lariniacantha grayi:—Archer, 1951: 15, figs. 38–40, ♀, ♂. Misidentification, not *Epeira grayi* Blackwall.

Araneus bicornuta:—Bonnet, 1955: 443.

Description. Female. Carapace, sternum orange. Legs orange with black tarsi. Dorsum of abdomen with white bands, black spot posteriorly. Carapace wide. Abdomen pointed behind with two anterolateral spines (Figs. 13, 15, 16). Total length 8.2 mm. Carapace 3.4 mm long, 2.7 wide. First femur 3.3 mm; patella and tibia 4.2; metatarsus 2.7; tarsus 1.1. Second patella and tibia 3.6 mm; third 2.2; fourth 3.7.

Male. Coloration as in female. Fourth trochanters with two macrosetae. Abdomen oval, without spines. Total length 5.7 mm. Carapace 3.0 mm long, 2.5 wide. First femur 2.9 mm; patella and tibia 3.5; metatarsus 1.9; tarsus 0.9. Second patella and tibia 2.8 mm; third 1.8; fourth 2.9.

Variation. Females are from 5.5 to 10.9 mm total length, males from 4.7 to 7.7. The living specimen photographed (Plate 1) had the carapace orange, legs gray, the abdomen with three rows of yellow patches on orange, black posterior and sides. The dorsum of the female abdomen may be

dark red and white, the carapace, in specimens from Costa Rica, bright orange. The abdomen may have longitudinal bands (Figs. 15, 16); sometimes it has a median anterior hump (Fig. 15).

Except for Figures 15 and 16, the specimens illustrated and described come from Panama (MCZ).

Diagnosis. Females differ from similar species by the presence of two spines on the abdomen (Figs. 13, 15, 16), and the roughly triangular epigynum having a median longitudinal light band (Fig. 11). The males, which lack spines on the abdomen, differ by the sclerotized two triangular areas of the terminal apophysis and by the rectangular median apophysis, which lacks lobes and projections. The tegulum has a small bent tip (Fig. 18).

Natural History and Distribution. The species has been collected from mud-dauber wasp nests in Costa Rica, Panama, Colombia, and Ecuador. It has been found in wet second growth forest in Costa Rica, forest savanna in Guyana and on tea plants in Peru. The egg-sac is flat, round, and attached to vegetation. Kochalka (in letter) writes that in Paraguay *A. bicornuta* is usually found in vegetation about 2 m off the ground. The egg-sac is bright yellow, smooth, very tightly pressed to vegetation. The female guards eggs. This species is found from Costa Rica to Argentina (Map 2). McCook (1894) cites specimens from Biscayne Bay [Florida] in the Marx collection. As with most other Marx specimens, the locality is probably in error. In the MCZ is a female marked "Florida," Banks collection. Did it come from the Marx collection? There are no recent Florida records.

Records. COSTA RICA *Limón*: Tortugera Natl. Park (DU). *Heredia*: La Selva near Puerto Viejo (MCZ). *Puntarenas*: Corcovado Natl. Park (MCZ). PANAMA *Colón* and *Panamá*: Canal area, common (AMNH, MCZ). TRINIDAD Maracas Valley (AMNH). GUYANA Tumatumari (AMNH); Kartabo (AMNH); Canje Ikuruwa River (AMNH). FRENCH GUIANA Cayenne (AMNH). COLOMBIA *Meta*: 5 km W, 45 km W Villavicensio (CAS, AMNH); Río Orteguaz (AMNH). *Valle*: Buenaventura (CAS). *Putumayo*: Buena Vista (MCZ). ECUADOR *Esmeraldes*: 11 km SE San Lorenzo. *Napo*: Pompeya, Río Napo (MCZ); Tarapuy, Aguas Negras (MECN); Coca, Río Napo (MCZ); Pumacocha (MECN); Río Tarapuy (MECN); Shushufindi (AMNH). *Pichincha:* km 113, Via Puerto Quito (MECN); 47 km S Santo Domingo (MCZ). *Los Ríos*: Juan Montalvo (AMNH); San Carlos (MECN). *Cañar*: Yanayacu (MECN). *Bolívar*: Balzapamba (MCZ, AMNH). *Guayas*: Milagro (CAS); Guayaquil (CAS). PERU *Loreto*: Iquitos (MCZ). *Amazonas*: Río Alto Marañon between Ríos Campa and Nieva (AMNH). *Ucayalí*: Pucallpa (PAN); Boquerón, 470 m (AMNH). *Huánuco*: Tingo María (CAS, MCZ); Monzon Valley (CAS); Las Palmas (CAS); Cord. Azul, 1,400 m (AMNH); Divisoria, 1,700 m (AMNH). *Junín*: Utcuyacu, 1,600–2,200 m (AMNH); Pumamarca, 1,900 m (PAN). *Cuzco*: Chanchosmayo Vall. (AMNH); Ocongale (AMNH). BRA-

→

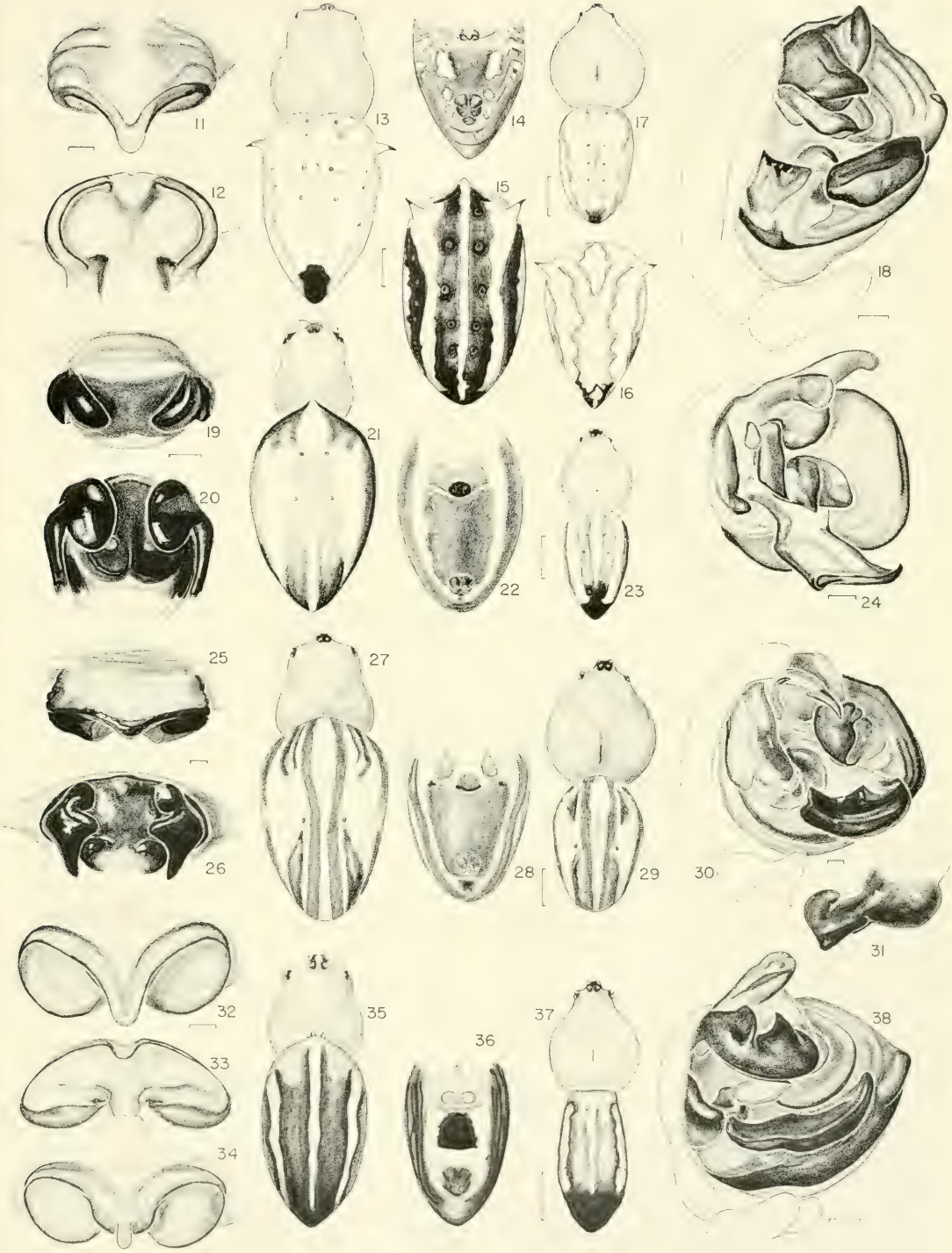
Figures 11–18. *Alpaida bicornuta* (Taczanowski). 11–16, female. 11, epigynum, ventral. 12, epigynum, posterior. 13, dorsal. 14–18, abdomen, ventral. 15, 16, abdomen, dorsal. 17, 18, male. 17, dorsal. 18, left palpus. 13, 14 (Panama). 15, (Peru). 16, (Ecuador).

Figures 19–24. *A. guimaraes* n. sp. 19–22, female 19, epigynum, ventral. 20, epigynum, posterior. 21, dorsal. 22, ventral. 23, 24, male. 23, dorsal. 24, palpus.

Figures 25–31. *A. utcuyacu* n. sp. 25–28, female. 25, epigynum, ventral. 26, epigynum, posterior. 27, dorsal. 28, ventral. 29–31, male. 29, dorsal. 30, palpus. 31, paracymbium, lateral.

Figures 32–38. *A. leucogramma* (White). 32–36, female. 32, 34, epigynum, ventral. 33, epigynum, posterior. 35, dorsal. 36, ventral. 37, 38, male. 37, dorsal. 38, palpus.

Scale lines. 1.0 mm, genitalia, 0.1 mm.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ZIL *Amazonas*: Manaus (NHRM). *Pará*: Jacareacanga (AMNH); Canindé (AMNH); Fordlândia (AMNH). *Acre*: Río Embira mouth (AMNH). *Bahia*: Camacã (MCN). *Goiás*: Pirenópolis (MZSP). *Mato Grosso*: Barra do Tapirapé (MZSP, AMNH); Chapada dos Guimarães (MCN); Barra dos Bugres (MNRJ). *Minas Gerais*: Lavras (MCZ). *Espírito Santo*: (BMNH). *Paraná*: Rolândia (AMNH). *Rio Grande do Sul*: São Borja (MCN). BOLIVIA *El Beni*: Espíritu, Yacuma (ZSM). *Cochabamba*: Yungas de Palmar, 1,000 m (ZSM). *La Paz*: Yungas, Coroico (IRSNB). PARAGUAY *Alto Paraná*: Taguarazapa (AMNH); Puerto Bertoni (MCZ). *Amambay*: Bella Vista (MNHNP). *Itapúa*: Capitan Meza (MNHNP). ARGENTINA *Misiones*: Parque Nacional Iguazu (MEG); Montecarlo (AMNH, MEG). *Corrientes*: Paso de la Patria (MEG). *Buenos Aires*: La Plata (MLP). *Río Negro*: El Bolson area (AMNH).

Alpaida guimaraes new species
Figures 19–24; Map 2

Holotype. Female from Chapada dos Guimarães, Mato Grosso, Brazil, 1 Dec. 1983, M. Hoffmann (MCN no. 11969). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange-yellow, sides darker orange, lateral eyes on black patches. Distal tips of chelicerae black. Labium orange with a black mark; endites orange with a black mark. Sternum orange with median black mark. Coxae orange; legs orange yellow dusky to black dorsally and ventrally, sides lighter. Dorsum of abdomen white, black and gray (Fig. 21); venter black with a white band on each side meeting behind spinnerets (Fig. 22). Eyes subequal in size. Anterior median eyes 1.2 diameters apart; posterior median eyes their diameter apart. Abdomen with small anterior median hump; pointed behind (Fig. 21). Total length 7.2 mm. Carapace 2.3 mm long, 1.6 wide. First femur 1.7 mm; patella and tibia 2.3; metatarsus 1.5; tarsus 0.6. Second patella and tibia 1.9 mm; third 1.2; fourth 1.9.

Male. Carapace dusky, coxae black; otherwise coloration similar to female. Eyes subequal in size. Anterior median eyes and posterior median eyes each their diameter apart. Total length 4.1 mm. Carapace 2.0 mm long, 1.7 wide. First femur 2.2 mm; patella and tibia 2.4; metatarsus 1.8; tarsus 0.9. Second patella and tibia 2.1 mm; third 1.1; fourth 1.7.

Notes. It is not certain that the male belongs with the female. The similar coloration, especially of legs and venter of abdomen, associates males and females.

There may be a median lobe on the epigynum that has been torn off in all available specimens.

Variation. Total length of females 5.2 to 7.2 mm. The illustrations and descriptions are from the holotype.

Diagnosis. The dark framing of the female abdomen in dorsal view (Fig. 21) resembles *A. utcuyacu*, but the two lateral lobes of the epigynum (Figs. 19, 20) are larger than those of *A. utcuyacu*. The median apophysis of the male palpus projects beyond the tegulum and subtegulum of the palpus, the terminal apophysis projects in the opposite direction (Fig. 24).

Distribution. Guyana to Mato Grosso, Brazil (Map 2).

Paratypes. GUYANA Kartabo, 1922, ♀ (AMNH). BRAZIL *Pará*: Jacareacanga, Oct. 1959, ♀ (M. Alvarenga, AMNH). *Bahia*: Fazenda Almada, Uruçuca, 26 Nov. 1977, ♂ (J. S. Santos, MCN 10287). *Mato Grosso*: Chavantina, Oct. 1946, ♀ (H. Sick, MZSP 4637); Barra dos Bugres, 3♀ (A. Cerrutti, MNRJ).

Alpaida utcuyacu new species
Figures 25–31; Map 2

Holotype. Female holotype and one male, one female paratypes from Utcuyacu, Junín, 1,600–2,200 m [near La Merced], Peru, March 1948 (F. Woytkowski, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange. Chelicerae orange, distally black. Labium, endites black. Sternum orange; coxae lighter orange. Proximal half of femora

orange, distal half and distal articles black. Dorsum of abdomen with symmetrical black and white streaks (Fig. 27); venter black behind genital groove (Fig. 28). Eyes subequal in size. Anterior median eyes 1.3 diameters apart; posterior medians slightly more than their diameter apart. Abdomen elongate. Total length 7.5 mm. Carapace 3.1 mm long, 2.4 wide. First femur 2.5 mm; patella and tibia 3.2; metatarsus 2.3; tarsus 0.9. Second patella and tibia 2.8 mm; third 1.7; fourth 2.7.

Male. Coloration as in female (Fig. 29). Anterior median eyes slightly larger than others. Fourth trochanters with two short macrosetae; second tibiae slightly thicker than first with macrosetae. Abdomen oval. Total length 6.8 mm. Carapace 3.4 mm wide, 2.9 long. First femur 3.3 mm; patella and tibia 3.9; metatarsus 2.6; tarsus 0.9. Second patella and tibia 2.9 mm; third 2.1; fourth 2.9.

Diagnosis. The color pattern, the two longitudinal median bands of the abdomen (Figs. 27, 29) and the shape of the lateral lobes of the epigynum (Figs. 25, 26) separate this species from *A. guimaraes*. The male differs from *A. guimaraes* by the median apophysis with two blunt teeth and the terminal apophysis hidden behind the embolus (Fig. 30).

Paratypes. Type locality: February 1948, ♀ (AMNH); 4 April 1948, ♀ (MCZ).

Alpaida leucogramma (White), new combination

Figures 32–38; Map 2

Epeira (Singa) leucogramma White, 1841: 474. Female holotype from near Rio de Janeiro, Brazil (C. Darwin, BMNH), examined.

Epeira albostriata Keyserling, 1865: 815, pl. 19, figs. 27, 28, ♀. Two female syntypes from N. Granada, [Spanish colony of Panama and Colombia] (BMNH), Keyserling, 1893: 258, pl. 13, fig. 193, ♀, ♂. NEW SYNONYMY.

Singa erythrothorax:—Taczanowski, 1873: 126. Male only, not female lectotype (PAN).

Araneus albostriata:—Tullgren, 1905: 34, pl. 5, fig. 11, ♀.

Aranea albostriata columbiana Strand, 1915: 110. Specimens from Popayan, Cauca, Colombia, lost. NEW SYNONYMY.

Parepeira albostriata:—Mello-Leitão, 1933: 41. Roewer, 1942: 871. Bonnet, 1958: 3433.

Singa leucogramma:—Roewer, 1942: 877.

Araneus leucogrammus:—Bonnet, 1955: 528.

Note. Keyserling overlooked White's description lacking illustrations of a specimen from Rio de Janeiro collected by Charles Darwin.

Description. Female from Panama. Carapace, sternum orange. Legs orange with black rings. Dorsum of abdomen with three white bands on orange-black (Fig. 35); venter with black square and dark spinnerets surrounded by white (Fig. 36). Abdomen oval (Fig. 35). Total length 5.8 mm. Carapace 2.5 mm long, 1.9 wide. First femur 1.8 mm; patella and tibia 2.2; metatarsus 1.4; tarsus 0.7. Second patella and tibia 2.0 mm; third 1.5. Fourth femur 2.0 mm; patella and tibia 2.3; metatarsus 1.4; tarsus 0.7.

Male. Coloration as in female, but first femur black. Abdomen truncate anterior (Fig. 37). Total length 5.5 mm. Carapace 2.7 mm long, 1.8 wide. First femur 2.0 mm; patella and tibia 2.5; metatarsus 1.6; tarsus 0.8. Second patella and tibia 2.0 mm; third 1.5. Fourth femur 2.1 mm; patella and tibia 2.5; metatarsus 1.7; femur 0.8.

Variation. Total length of females 4.9 to 6.5 mm, males 4.2 to 5.4. Southern specimens are larger than northern ones. A specimen from Panama had a secondary median lobe on the epigynum (Fig. 34). In posterior view the median plate may be longer (ventral–dorsally) than those illustrated by Figure 33. The head of southern specimens is usually black.

The description and illustration are from specimens from Barro Colorado Island, Panama (MCZ).

Diagnosis. The two round lateral lobes, one on each side of the scape of the epigynum in ventral view (Fig. 32); the elongate median apophysis of the male palpus, the projecting terminal apophysis and its sclerotized lobed base (Fig. 38) separates

A. leucogramma from *A. grayi* and other *Alpaida* with banded abdomens.

Natural History and Distribution. I have collected specimens from between grass blades of a closely cropped pasture in Colombia. The only other record with ecological data is from brush in São Luis, Pará, Brazil. The distribution is from Panama to Argentina (Map 2).

Records. PANAMA, *Coclé*: 10 km N El Copé (MIUP). *Colón*: Santa Rosa (AMNH). *Colón* and *Panamá*: Canal area, very common (AMNH, MCZ, MIUP). *Darién*: El Real de Santa Marta (AMNH). COLOMBIA *Magdalena*: 15 km E Pueblo Bello, 500 m (AMNH). *Antioquia*: Medellín (MCZ); Santa Fé de Antioquia, 200 m (MCZ). *Meta*: Villavicensio (AMNH). *Valle*: Río Pauce (MCZ); Cali (MCZ); Lago Calima (MCZ). ECUADOR *Pichincha*: 47 km S Santo Domingo (MCZ). *Guayas*: Guayaquil (CAS); Milagro (CAS). PERU *Loreto*: Iquitos (MCZ). *Cajamarca*: Jaén (AMNH). *San Martín*: E of Tarapato (AMNH). BRAZIL *Pará*: Belém (MEG). *Amazonas*: Igarapé Belém confl. Rio Solimões (AMNH); Alto Solimões (MCN). *Mato Grosso*: Barra do Tapirapé (AMNH); Cuiabá (AMNH). *Rio de Janeiro*: Rio de Janeiro (ZMK). Rio Grande (AMNH). *São Paulo*: Morro do Serrote, Juquiá (MZSP); Aldeia (MZSP). *Rio Grande do Sul*: São Leopoldo (MZSP); Montenegro (MCN); Itaubá (MCN); Canela (MCN); Bajé (MCN). URUGUAY. Montevideo (MCZ, MNHM). PARAGUAY. *Concepción*: San Luiz (AMNH). *Presidente Hayes*: 25 Lagua (MNHNP). ARGENTINA. *Misiones*: Eldorado (AMNH); San Ignacio (MEG). *Salta*: Agua Blanca (MEG). *Córdoba*: Calamuchita (MACN). *La Pampa*: Santa Rosa (MACN). *Neuquen*: El Hueco (MCZ).

Alpaida coroico new species
Figures 39–43; Map 2

Holotype. Male from Coroico, Dpto. La Paz, Bolivia, 8 June 1960 (B. Malkin, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, coxae orange. Legs with proximal two-thirds of femora orange, distal third and distal articles black. Dorsum of abdomen black with symmetrical white bordered orange marks (Fig. 41); venter black. Anterior median eyes slightly more than their diameter apart; posterior median eyes their diameter apart. Abdomen oval. Total length 7.2 mm. Carapace 2.8 mm long, 2.3 wide. First femur 2.3 mm; patella and tibia 2.7; metatarsus 1.8; tarsus 0.8. Second patella and tibia 2.5 mm; third 1.5; fourth 2.4.

Male. Coloration as in female, except for a median black patch on the thoracic groove (Fig. 42) and black articles of legs, which are orange anterior and posterior. Second tibiae slightly thicker than first and proximally swollen with about five pairs of ventral macrosetae; fourth trochanters with two small macrosetae. Total length 7.2 mm. Carapace 3.6 mm long, 2.9 wide. First femur 3.1 mm; patella and tibia 3.7; metatarsus 2.3; tarsus 0.9. Second patella and tibia 2.9 mm; third 1.9; fourth 2.9.

Note. Male and female were matched because of similar markings and proximity of collecting sites.

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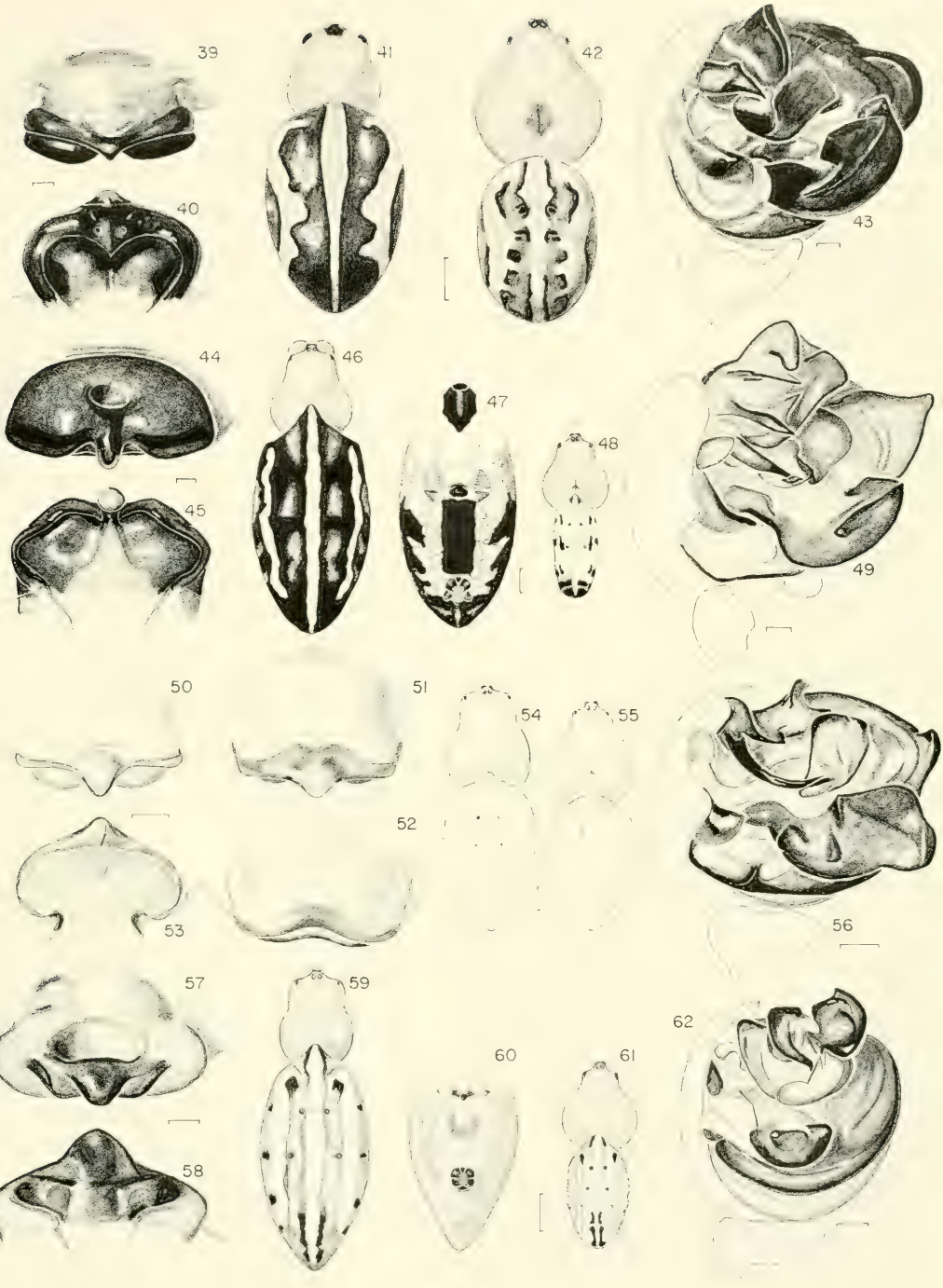
Figures 39–43. *Alpaida coroico* n. sp. 39–41, female. 39, epigynum, ventral. 40, epigynum, posterior. 41–42, male. 41, dorsal. 42, left palpus.

Figures 44–49. *A. grayi* (White). 44–47, female. 44, epigynum, ventral. 45, epigynum, posterior. 46, dorsal. 47, ventral. 48, 49, male. 48, dorsal. 49, palpus.

Figures 50–56. *A. rostratula* (Keyserling). 50–54, female. 50–52, epigynum, ventral. 52, median, lobe torn off. 53, epigynum, posterior. 54, dorsal. 55, 56, male. 55, dorsal. 56, palpus.

Figures 57–62. *A. rubellula* (Keyserling). 57–60, female. 57, epigynum, ventral. 58, epigynum, posterior. 59, dorsal. 60, ventral. 61–62, male. 61, dorsal. 62, palpus.

Scale line. 1.0 mm; genitalia, 0.1 mm.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Diagnosis. The lateral lobes of the paraxial dark band of the abdomen (Figs. 41, 42) separate the species from *A. leucogramma* and *A. grayi*. The epigynum, unlike that of related species, has a convex bilobed posterior median plate (Figs. 39, 40); the male palpus has an apically pointed terminal apophysis, a small lobe on the distal border of the embolus, and a broadly lobed tegulum (Fig. 43).

Paratypes. BOLIVIA *La Paz*: Chulumani, 1,700 m, 17–25 Dec. 1955, ♀ (L. Peña, IRSNB).

Alpaida grayi (Blackwall)
Figures 44–49; Map 2

Epeira grayi Blackwall, 1863: 34. Six female and three males from Rio de Janeiro, Brazil, marked "type" (BMNH), examined. Keyserling, 1892: 79, pl. 4, fig. 60, ♀ [not Keyserling, 1865: 809, pl. 18, figs. 9, 10].

Epeira veles Keyserling, 1880: 310, pl. 4, fig. 12. Female from Neu Freiburg [Nova Friburgo, Est. Rio de Janeiro], Brazil. First synonymized by Keyserling, 1892.

Aranea grayii:—Roewer, 1942: 844.

Lariniacantha grayi:—Archer, 1951: 15.

Araneus grayi:—Bonnet, 1955: 511.

Description. Female. Carapace orange. Chelicerae orange, dark brown distally; labium, endites black; sternum black with median longitudinal light streak. Coxae orange, legs ringed black and orange. Dorsum of abdomen with three longitudinal white bands bordered by black (Fig. 46); venter with rectangular black patch (Fig. 47). Abdomen elongate oval with anteromedian hump and two slight lateral humps. Total length 10.8 mm. Carapace 4.2 mm long, 3.1 wide. First femur 3.7 mm; patella and tibia 4.6; metatarsus 3.2; tarsus 1.4. Second patella and tibia 4.0 mm; third 2.7; fourth 4.2.

Male. Coloration as in female (Fig. 48). Second tibiae swollen, with macrosetae. Total length 7.4 mm. Carapace 3.7 mm long, 2.7 wide. First femur 3.5 mm; patella and tibia 4.2; metatarsus 2.9; tarsus 1.0. Second patella and tibia 3.4 mm; third 2.5; fourth 3.7.

Variation. Total length of females 7.8 to 14.0 mm; of males 7.2 to 10.1.

The description and illustrations are from syntype specimens of *veles* (BMNH).

Diagnosis. This species is of larger size than *A. leucogramma* and the epigynum differs by being a sclerotized semicircular projection with a notch on its anterior surface (Fig. 44); the male palpus by having a shorter median apophysis and the tegulum with a drawn out point (Fig. 49).

Records. BRAZIL *Rio de Janeiro*: Petrópolis, 850 m (AMNH); Teresópolis, 900–1,290 m (AMNH); Itatiaia (AMNH, MZSP). *São Paulo*: Salesópolis (AMNH, MZSP); São Paulo (MZSP); Itanhaém (MZSP); Boracéia (MZSP); Campos de Jordão (MZSP); Iporanga (MZSP); Alto Serra (MZSP). *Paraná*: Foz de Iguaçu (MCZ, AMNH); Curitiba (MZSP); Marumbi (MNRJ). *Santa Catarina*: Corupá (AMNH); Pinhal (AMNH); Blumenau (MCZ, MZSP). *Rio Grande do Sul*: [?] S Féo de Paula (MNRJ); Porto Alegre (MCN); Cambará do Sul (MCN). ARGENTINA *Misiones*: Eldorado (AMNH); Iguazu (MEG); Arroyo El Central, San Antonio (MEG); Gral. Manuel Belgrano (MEG); Monte Carlo (AMNH).

Alpaida rostratula (Keyserling), new combination
Figures 50–56; Map 2

Epeira rostratula Keyserling, 1892: 82, pl. 4, fig. 62, ♂. Male holotype and juvenile female paratype from Taquara, Est. Rio Grande do Sul, Brazil (BMNH), examined.

Aranea rostratula:—Roewer, 1942: 651.

Araneus rostratulus:—Bonnet, 1955: 586.

Description. Female. Carapace, sternum, legs yellow-white. Dorsum of abdomen whitish with parallel indistinct longitudinal streaks (Fig. 54); venter of abdomen yellow-white, sides white. Eyes small. Anterior median eyes twice their diameter apart; posterior median eyes slightly more than twice their diameter apart. Abdomen elongate oval with anterior median hump (Fig. 54). Total length 5.2 mm. Carapace 2.3 mm long, 1.8 wide. First femur 2.0 mm; patella and tibia 2.3; metatarsus 1.4; tarsus 0.7. Second patella and tibia 2.1 mm; third 1.3; fourth 1.9.

Male. Coloration as in female. Dorsum of abdomen with three white streaks. Palpal patella with one large macroseta and one smaller one. Abdomen oval. Total length 4.1 mm. Carapace 2.0 mm long, 1.7 wide. First femur 1.9 mm; patella and tibia 2.3; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.8 mm; third 1.1; fourth 1.8.

Variation. Total length of females varies from 4.9 to 7.2 mm. The tip of the epigynum is torn off in some females (Fig. 52).

Diagnosis. The small eyes, light color, lightly sclerotized epigynum (Figs. 50–53) and the large squarish median apophysis and small terminal apophysis of the male palpus (Fig. 56) separate the species from *A. rubellula.*

The description and illustrations are from specimens from Rio Grande do Sul (MCN), Fig. 52 from Salta (MACN).

Records. BRAZIL *Rio Grande do Sul*: Canela, 11 Jan. 1966, ♂ (A. A. Lise, MCN 216); Rio Pardo, 10 Feb. 1969, ♀ (A. A. Lise, MCN 410); Cambará do Sul, 9 Jan. 1976, 2♀, 6♂, 6 imm. (A. A. Lise, MCN 3354), 15 Jan. 1978, 5♂ (P. C. Braum, MCN 7713). ARGENTINA *Salta*: ♀ (MACN 8492). *Buenos Aires*: Río de la Plata, Isla Martin García, Apr. 1938 (M. J. Viana, MACN 8493).

Alpaida rubellula (Keyserling), new combination
Figures 57–62; Map 2

Epeira rubellula Keyserling, 1892: 81, pl. 4, fig. 61, ♀. Female holotype from Rio Grande do Sul, Brazil (BMNH), examined.

Araneus inexplicabilis Badcock, 1932: 23, fig. 16, ♀. Female from Nanahua, Chaco, Paraguay, near Bolivian border, [Nanawa, Fortín Presidente Ayala, Dpto. Presidente Hayes] (BMNH), examined. Bonnet, 1955: 522. NEW SYNONYMY.

Wixia nigropunctata Mello-Leitão, 1941b: 214, figs. 21, 22, ♀. Female from El Rabón, Prov. Santa Fé, Argentina (MLP), examined. Brignoli, 1983: 281. NEW SYNONYMY.

Wixia albotaeniata Mello-Leitão, 1942: 403, figs. 25, 26, ♀. Female from Basail, Prov. Chaco, Argentina, (MLP), examined. Brignoli, 1983: 281. NEW SYNONYMY.

Aranea inexplicabilis:—Roewer, 1942: 845.

Aranea rubellula:—Roewer, 1942: 851.

Araneus rubellulus:—Bonnet, 1955: 586.

Description. Female. Carapace, sternum orange. Legs orange with narrow black rings at end of articles. Dorsum of abdomen with three white, longitudinal bands in between black spots (Fig. 59); sides with dorsoventral white marks; venter orange gray with only indistinct, dusky marks (Fig. 60); black spinnerets. Abdomen oval, with anterior median hump, posteriorly pointed, sides slightly scalloped (Fig. 60). Total length 8.0 mm. Carapace 2.7 mm long, 2.1 wide. First femur 2.1 mm; patella and tibia 2.7; metatarsus 1.5; tarsus 0.8. Second patella and tibia 2.3 mm; third 1.5; fourth 2.5.

Male. Coloration as in female (Fig. 61). Second tibiae with macrosetae. Abdomen oval. Total length 4.8 mm. Carapace 2.3 mm long, 1.8 wide. First femur 2.1 mm; patella and tibia 2.5; metatarsus 1.4; tarsus 0.6. Second patella and tibia 1.9 mm; third 1.3; fourth 2.1.

Variation. Total length of females 6.6 to 8.5 mm, males 4.9 to 5.3. The lobe of the epigynum is torn off in some females, including the type specimen of *A. inexplicabilis.*

The description and illustrations are of specimens from Paraguay (MCZ).

Diagnosis. Females are similar to *A. trispinosa* and *A. keyserlingi* but lack anterior spines on the abdomen (Fig. 59). Unlike *A. rostratula*, the epigynum has a wide notch (Fig. 57). The male palpus has a much shorter embolus (Fig. 62) than the two similar species.

Natural History. Kochalka (in letter) states that, like *A. bicornuta*, *A. rubellula* is found in vegetation about 2 m off the ground. The egg-sac is bright yellow, smooth, and very tightly pressed against the vegetation. It is guarded by the female.

Records. BRAZIL *Mato Grosso*: Chapada dos Guimarães (MCN). *Goiás*: Aragarças (MZSP). *Rio Grande do Sul*: Parque Est. de Nonoai (MCN); Garruchos São Borja (MCN); Quaraí (MCN); Santa Rosa (MCN). PARAGUAY *Concepción*: Con-

cepción (MCZ). *Alto Paraná*: Puerto Bertoni (MCZ). *La Cordillera*: San Bernardino (MCZ). *Itapúa*: 20 km NNE Puerto Capitán Meza (MCZ). *Central*: Luque (MNHNP); San Lorenzo (MNHNP, MCZ). ARGENTINA *Misiones*: Iguazu (MEG); Eldorado (AMNH). *Salta*: Orán (MEG). *Chaco*: Roque Sáenz Peña (MLP). *Córdoba*: Calamuchita (MACN); [?] Altos Pampa (MLP). *Mendoza*: San Luis Chosmes (MCZ); ? Canigal (MACN). *Río Negro*: El Bolson (AMNH).

Alpaida trispinosa (Keyserling), new combination
Figures 63–68; Map 2

Epeira grayi:—Keyserling, 1865: 809, pl. 18, figs. 9, 10. Misidentification, not *grayi* Blackwall.

Epeira trispinosa Keyserling, 1892: 78, pl. 4, fig. 59, ♀, ♂. Specimens from Miracena, Serra Vermelha, Est. Rio de Janeiro, Uruguay and New Granada, (BMNH). Female lectotype from Rio de Janeiro here designated and one female, one male paralectotype of this species and three female, two male paralectotypes that are *A. keyserlingi*.

Aranea trispinosa:—Roewer, 1942: 854.

Araneus trispinosus:—Bonnet, 1955: 619.

Note. Keyserling's description and illustrations appear to be a composite of this species and *Alpaida keyserlingi*. I chose a lectotype for the name *trispinosa* of the more common and widespread species.

Description. Female from Paraguay. Carapace light orange-brown with a median dark line; sternum, legs light orange-brown; legs with narrow black rings. Dorsum of abdomen with three white bands on gray and a pair of black spots on posterior (Fig. 65); venter with indistinct gray marks (Fig. 66). Abdomen elongate with three anterior spines (Fig. 65). Total length 6.2 mm. Carapace 1.9 mm long, 1.4 wide. First femur 1.8 mm; patella and tibia 2.0; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.7 mm; third 1.1; fourth 2.0.

Male from Paraguay. Coloration as in female (Fig. 67). Fourth coxae with three to four macrosetae; fourth trochanters with two macrosetae. Abdomen elongate with median anterior hump (Fig. 67), but no spines. Total length 4.8 mm. Carapace 2.0 mm long, 1.5 wide. First femur 2.0 mm; patella and tibia 2.4; metatarsus 1.5; tarsus 0.7. Second patella and tibia 1.7 mm; third 1.1; and fourth, 2.2.

Variation. Total length of females 4.5 to 6.7 mm, males 3.6 to 5.3. The descriptions and illustrations are from specimens from Paraguay (MCZ).

Diagnosis. Females differ from most *Alpaida* by having three anterior spines on the abdomen, the median one anterior to the laterals (Fig. 65), from *A. keyserlingi* and *A. monzon* by having the epigynum with a rounded median lobe framed by a lobe on each side in ventral view (Fig. 63). The male differs by having the embolus of the palpus coiled, a relatively small laterally pointing terminal apophysis and the median apophysis with a giant projecting tooth (Fig. 68).

Natural History and Distribution. Specimens have been collected in vegetation on stream banks in northern Colombia; in campo-grassland in Mato Grosso. *Alpaida trispinosa* is found from Panama to Argentina, and is most common in southern Brazil (Map 2).

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Figures 63–68. *Alpaida trispinosa* (Keyserling). 63–66, female. 63, epigynum, ventral. 64, epigynum, posterior. 65, dorsal. 66, ventral. 67, 68, male. 67, dorsal. 68, left palpus.

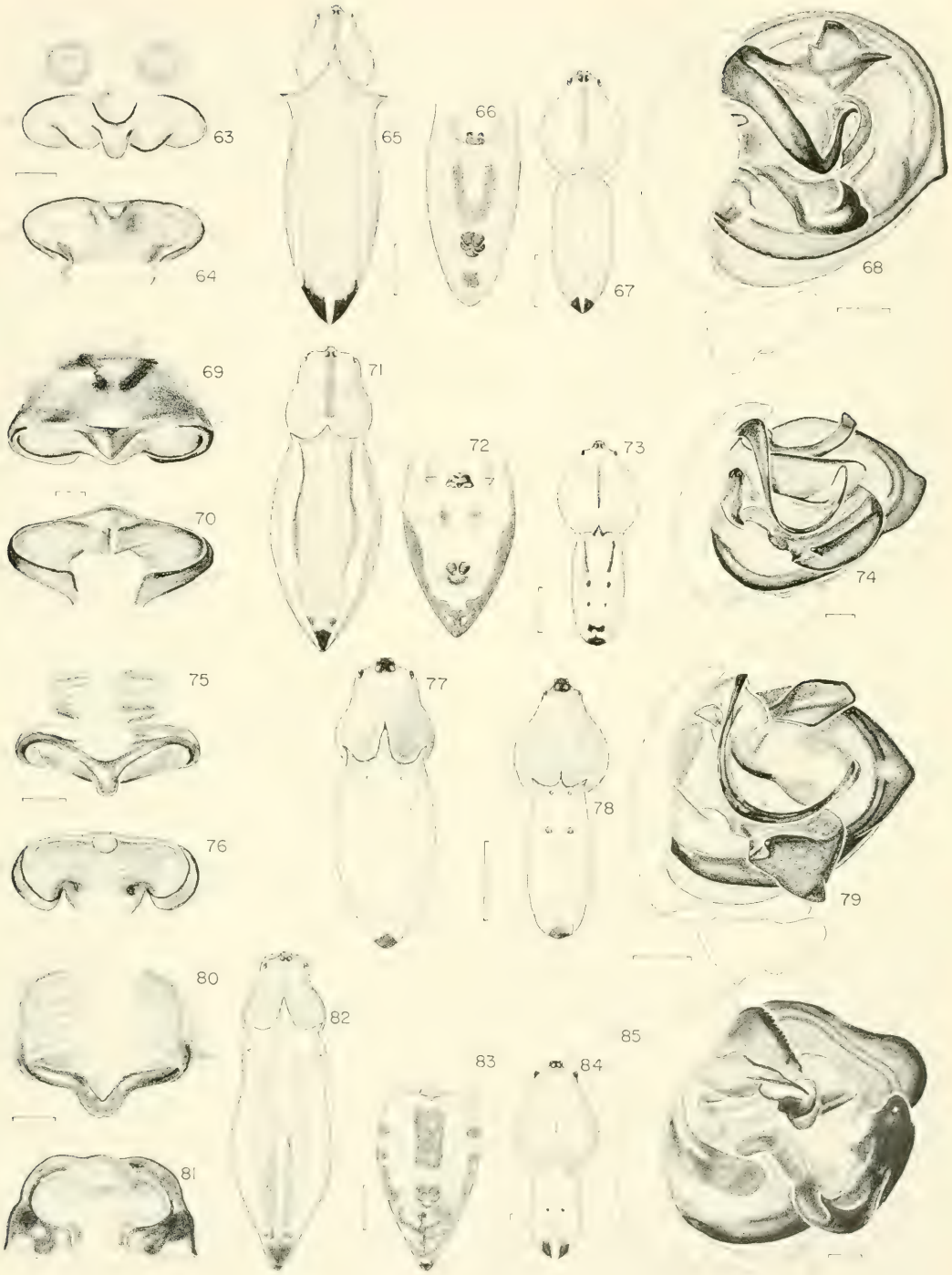
Figures 69–74. *A. keyserlingi* n. sp. 69–72, female. 69, epigynum, ventral. 70, epigynum, posterior. 71, dorsal. 72, ventral. 73, 74, male. 73, dorsal. 74, palpus.

Figures 75–79. *A. monzon* n. sp. 75–77, female. 75, epigynum, ventral. 76, epigynum, posterior. 77, dorsal. 78, 79, male. 78, dorsal. 79, palpus.

Figures 80–83. *A. kartabo* n. sp., female. 80, epigynum, ventral. 81, epigynum, posterior. 82, dorsal. 83, ventral.

Figures 84, 85. *A. murtinho* n. sp., male. 84, dorsal. 85, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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Records. PANAMA *Chiriquí*: Playa las Lajas, (MIUP). *Colón*: Fort Sherman (MCZ). *Panamá*: Summit (AMNH). LESSER ANTILLES *Trinidad*: St. Augustine Univ. campus (MCZ). COLOMBIA *Magdalena*: Río Don Diego, 70 km E of Santa Marta (SMF). *Cesar*: Valledupar (AMNH). *Antioquia*: Santa Fé de Antioquia, Río Cauca, 700 m (MCZ); Mutatá (MCZ). *Valle*: Cali, 1,000 m (MCZ). *Vaupés*: Mitú, 200 m (MCZ). BRAZIL *Amazonas*: Manaus, Ponta Negra (MEG). *Mato Grosso*: 260 km N Xavantina, 12°49′S, 51°46′W (MCZ). *Rio de Janeiro*: Rio de Janeiro (AMNH); S. Antonio do Imbe, S. Maria Madalena (AMNH). *Rio Grande do Sul*: Santa Rosa (AMNH); Santa Maria (MCN). PARAGUAY *Concepción*: Territ. Foncière (MCZ). *Caazapá*: Pastoreo (MCZ). *Paraguarí*: San Luis (AMNH). ARGENTINA *Misiones*: Eldorado (AMNH). *Salta*: NE of Salta, 350–1,500 m (MCZ).

Alpaida keyserlingi new species
Figures 69–74; Map 2

Holotype. Female holotype, three females, one male and three immature paratypes from Rio de Janeiro, Brazil (BMNH). The species is named after the arachnologist, who had mislabeled the specimens.

Note. All BMNH specimens are paralectotypes of *Epeira trispinosa* Keyserling.

Description. Female. Carapace yellowish with a median dusky line. Sternum, coxae, legs yellowish. Dorsum of abdomen with three white stripes (Fig. 71) and posterior black spot; venter with dark spinnerets, sides and posterior dusky. Abdomen with three spines on truncate anterior. Total length 7.0 mm. Carapace 2.5 mm long, 2.0 wide. First femur 2.1 mm; patella and tibia 2.5; metatarsus 1.8; tarsus 0.6. Second patella and tibia 2.1 mm; third 1.5; fourth 2.2

Male. Coloration as in female but less white, more black on the abdomen (Fig. 73). Fourth coxae with a short macroseta. Abdomen as in female. Total length 5.0 mm. Carapace 2.2 mm long, 1.9 wide. First femur 2.1 mm; patella and tibia 2.5; metatarsus 1.5; tarsus 0.7. Second patella and tibia 2.1 mm; third 1.3; fourth 2.0.

Variation. Females vary in total length from 5.6 to 7.8 mm, males from 3.9 to 5.0.

The specimens described and illustrated are from the holotype and paratypes (BMNH).

Diagnosis. Females differ from *A. trispinosa* by having the three abdominal spines in a row (Fig. 71) and the epigynum with a more pointed median lobe, lacking the lobe on each side (in ventral view Fig. 69). Males differ from *A. trispinosa* and *A. monzon* by having a curved bar as terminal apophysis and having a longer median apophysis in the palpus (Fig. 74).

Paratypes. BRAZIL *Rio de Janeiro:* Duque de Caxias, Sept. 1961, 7♂, 4♀; Silva Jardim, Aug. 1975, 2♂, 3♀; Nova Iguaçu, 7 Sept. 1961, 3♂; Muriqui, Manaratiba, Oct. 1961, several ♂, ♀ (all M. Alvarenga, AMNH). *São Paulo*: Caraguatatuba 2 Apr. 1962, ♀ (K. Lenko, MZSP 7797), July 1965, 6♀ (Exp. Dept. Zool., MZSP 4935, 4693).

Alpaida monzon new species
Figures 75–79; Map 2

Holotype. Female from Monzón Valley, Tingo María, Dpto. Huánuco, Peru, 23 Sept. 1954 (E. I. Schlinger, E. S. Ross, CAS). The specifc name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, coxae orange-yellow. Second femora mostly black; legs with wide black rings. Dorsum of abdomen with two white streaks, one each behind each lateral anterior spine; posterior tip black; spinnerets black. Posterior median eyes 1.5 times diameter of anterior median eyes; anterior lateral eyes 0.6; posterior lateral eyes 0.8. Abdomen elongate with three anterior spines (Fig. 77), covered with scattered setae. Total length 3.8 mm. Carapace 1.6 mm long, 1.3 wide. First femur 1.7 mm; patella and tibia 1.9; metatarsus 1.2; tarsus 0.6. Second patella and tibia 1.5; third 0.9; fourth 1.5.

Male. Coloration as in female; legs darker. Venter of abdomen dusky to black. Eyes

as in female. Abdomen as in female, with three teeth anterior and setae (Fig. 78). Second tibia not swollen. Total length 3.5 mm. Carapace 1.6 mm long, 1.3 wide. First femur 1.8 mm; patella and tibia 1.8; metatarsus 1.1; tarsus 0.5. Second patella and tibia 1.3; third 0.9; fourth 1.3.

Variation. Females vary in total length from 3.8 to 5.5 mm.

Diagnosis. Females have longer spines than *A. trispinosa* and *A. keyserlingi* and the spines are in a transverse row (Fig. 77); the epigynum (Figs. 75, 76) differs from *A. trispinosa* by having a distinct lip, from *A. keyserlingi* by having a rounded lobe. Males differ from *A. keyserlingi,* which also has three anterior spines on the abdomen, by the shape of the median apophysis (Fig. 79).

Paratypes. Type locality, 19 Oct. 1954, ♀, ♂ (E. I. Schlinger, E. I. Ross, CAS).

Alpaida kartabo new species
Figures 80–83; Map 2

Holotype. Female from Kartabo, Bartica District, Guyana, 1920 (AMNH). The specific name is a noun in apposition after the locality.

Note. Specimen discolored from storage in cork-stoppered vials.

Description. Female. Carapace with yellow median dusky line and rim of thorax with dusky band. Sternum, legs yellow. Dorsum of abdomen with longitudinal bands, posterior tip black (Fig. 82); venter without pigment except for rectangular dusky patch between epigynum and spinnerets, maculated black behind spinnerets. Posterior median eyes 1.4 diameters of others, which are subequal in size. Anterior median eyes 1.5 their diameter apart; posterior median eyes their diameter apart. Abdomen elongated, pointed behind with five anterior spines (Fig. 82). Total length 7.4 mm. Carapace 2.5 mm long, 2.0 wide. First femur 2.6 mm; patella and tibia 2.9; metatarsus 2.2; tarsus 1.0. Second patella and tibia 2.5 mm; third 1.6; fourth 2.5.

Note. Epigynum has a seam where distal part may break off.

Diagnosis. The female is distinguiished from *A. monzon* and related species by two additional spines at the anterior end of the abdomen (Fig. 82) and by the wider median lobe containing the notch of the epigynum (Fig. 80).

Alpaida murtinho new species
Figures 84, 85; Map 2

Holotype. Male from Vila Murtinho, Rondônia, Brazil, 3 April 1922 (J. H. Williamson, ex MCZ, MZSP). The specific name is a noun in apposition after the locality.

Description. Male. Carapace orange; sternum orange with dusky mark in middle. Legs yellow-white with dorsal longitudinal dark line. Dorsum of abdomen with three longitudinal white lines and a pair of black patches on posterior end (Fig. 84); venter black. Fourth trochanters with a short macroseta. Abdomen shield-shaped, pointed behind. Total length 4.8 mm. Carapace 2.7 mm long, 2.1 wide. Third patella and tibia 1.5 mm; fourth 2.4.

Note. This male, unlike others, has a joint between radix and embolus-terminal apophysis; it may not belong in the genus *Alpaida.*

Diagnosis. This male differs from *A. leucogramma* and *A. coroico* by the shape of the median apophysis, a distal lobe and proximal point, and the denticles on the distal margin of the small terminal apophysis (Fig. 85).

Alpaida cuiaba new species
Figures 86–89; Map 2

Holotype. Female from Cuiabá, Mato Grosso, Brazil, Nov. 1963 (M. Alvarenga, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, coxae, legs orange. Dorsum of abdomen banded black and white (Fig. 88); venter with black patch on orange, spinnerets brown with black ring around spinnerets and a black band under overhang behind spinnerets (Fig. 89). Abdomen oval, rounded in front, elongate behind spinnerets (Fig. 89). Total length 5.6 mm. Carapace 1.9 mm, 1.3 wide. First femur 1.7 mm; patella and tibia 1.9; metatarsus 1.3;

tarsus 0.6. Second patella and tibia 1.6 mm; third 0.9; fourth 1.7.

Diagnosis. The female is distinguished from *A. chapada* and other similar species by the abdomen, extended into a tail posterior to the spinnerets (Figs. 88, 89), and by the notch anterior to the median lobe of the epigynum (Fig. 86).

Alpaida cachimbo new species
Figures 90, 91; Map 2

Holotype. Male from 260 km N of Xavantina, 12°49'S, 51°46'W, 400 m, Est. Mato Grosso, Brazil, Feb.–Apr. 1969 (Xavantina-Cachimbo Expedition, ex MCZ, MZSP). The specific name is a noun in apposition after the locality.

Description. Male. Carapace dark orange; sternum orange. Legs dusky orange. Dorsum of abdomen with three white longitudinal lines and three pairs of black marks (Fig. 90); venter dusky orange, spinnerets black, and, posteriorly, a black longitudinal band under overhang. Eyes small. Anterior median eyes 1.5 their diameter apart; posterior median eyes their diameter apart. Second tibiae not modified. Abdomen elongate, rounded behind. Total length 3.0 mm. Carapace 1.3 mm long, 0.9 wide. First femur 1.5 mm; patella and tibia 1.7; metatarsus 1.2; tarsus 0.5. Second patella and tibia 1.3 mm; third 0.7; fourth 1.2.

Natural History. The specimen was collected in campo-grassland.

Diagnosis. The male is distinguished from others by the even U-shaped curvature of the long embolus (Fig. 91).

Alpaida hoffmanni new species
Figures 92–96; Map 2

Holotype. Female from Chapada dos Guimarães, Mato Grosso, Brazil, 18 Nov. 1983, ♀ (M. Hoffmann, MCN no. 11977). The species is named after the collector.

Description. Female. Carapace yellow with indistinct paired dusky marks. Sternum, coxae yellow. Legs yellow with narrow ring on distal end of all articles, those on femur broken ventrally. Dorsum of abdomen with paired pigmentless scalloped marks; sides dorsally white, a small black spot two-thirds toward posterior tip (Fig. 94); venter yellowish gray without pigment. Anterior median eyes slightly more than their diameter apart; posterior median eyes their diameter apart. Abdomen elongate, pointed behind with shoulder humps and anterior median hump. Total length 7.2 mm. Carapace 2.5 mm long; 1.9 wide. First femur 2.3 mm; patella and tibia 2.8; metatarsus 1.9; tarsus 0.7. Second patella and tibia 2.4 mm; third 1.5; fourth 2.5.

Male. Coloration as in female, with legs dusky. Dorsum marked as in Figure 95; venter black in between genital area and spinnerets; sides orange. Second tibiae as thick as first. Total length 3.4 mm. Carapace 1.8 mm long, 1.5 wide. First femur 1.7 mm; patella and tibia 1.8; metatarsus 1.1; tarsus 0.6. Second patella and tibia 1.5 mm; third 1.0; fourth 1.6.

Note. It is uncertain if the male belongs with the female.

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Figures 86–89. *Alpaida cuiaba* n. sp., female. 86, epigynum, ventral. 87, epigynum, posterior. 88, dorsal. 89, ventral.

Figures 90, 91. *A. cachimbo* n. sp., male. 90, dorsal. 91, left palpus.

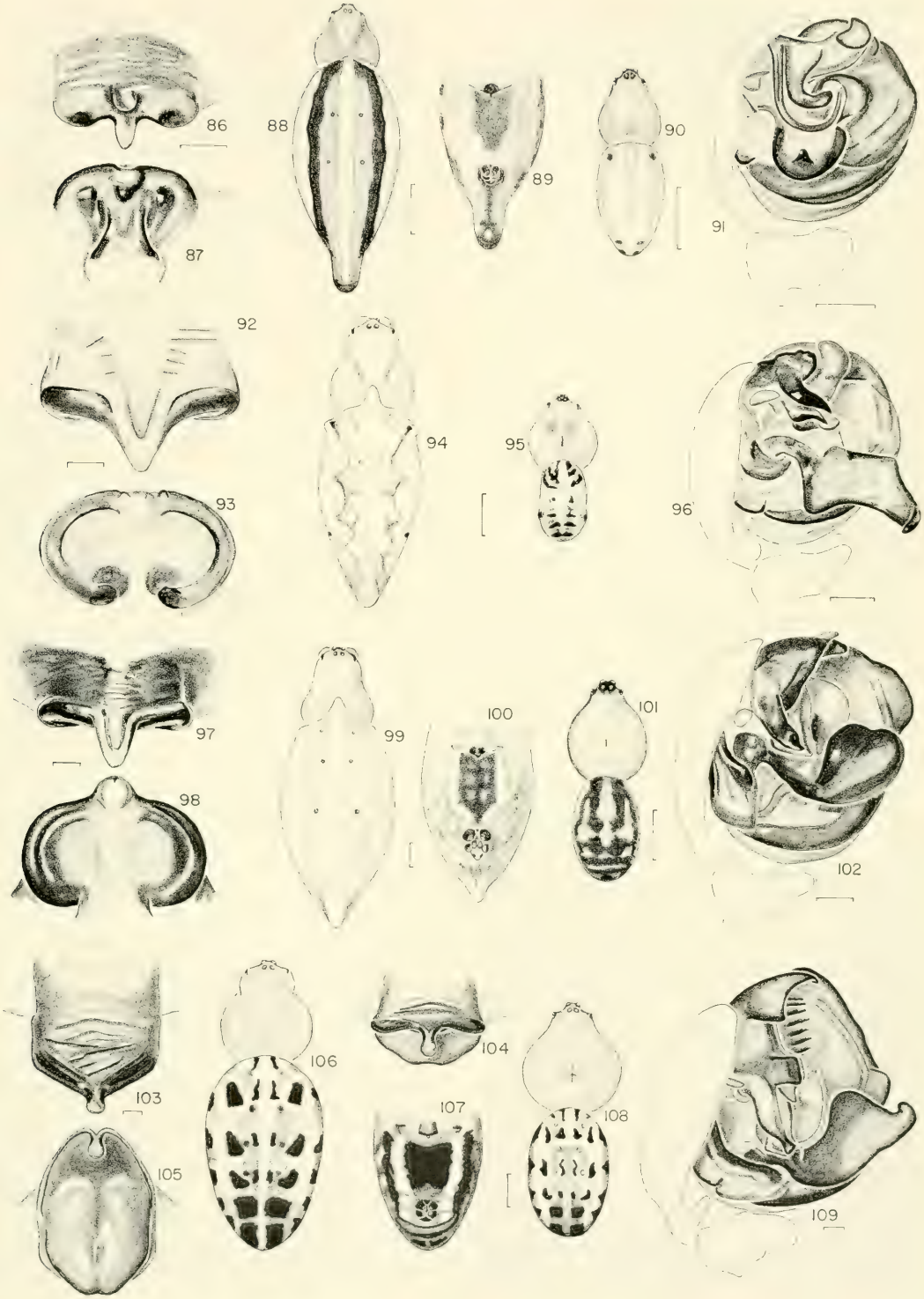
Figures 92–96. *A. hoffmanni* n. sp. 92–95, female. 92, epigynum, ventral. 93, epigynum, posterior. 94, dorsal. 95, 96, male. 95, dorsal. 96, palpus.

Figures 97–100. *A. chapada* n. sp., female. 97, epigynum, ventral. 98, epigynum, posterior. 99, dorsal. 100, ventral.

Figures 101, 102. *A. constant* n. sp., male. 101, dorsal. 102, palpus.

Figures 103–109. *A. veniliae* (Keyserlingi). 103–106, female. 103, epigynum, anterior. 104, epigynum, ventral. 105, epigynum, posterior. 106, dorsal. 107, ventral. 108, 109, male. 108, dorsal. 109, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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Variation. Total length of females from 6.0 to 7.2 mm, males from 3.2 to 3.4.

The description and illustrations are of the holotype and a male from Mato Grosso (MCN).

Diagnosis. The scalloped markings on the female abdomen (Fig. 94), the epigynum whose median lobe is not distinctly set off (Fig. 92) and two dorsal, round, dark marks in posterior view (Fig. 93) separate the females from others. Males differ by the large, curved, projecting median apophysis of the palpus (Fig. 96).

Paratypes. BRAZIL *Bahia*: Encruzilhada, 960 m, Nov. 1973, ♂ (M. Alvarenga, AMNH). *Mato Grosso do Sul*: Três Lagôas, 1964, ♀ (C. D. Z., MZSP 3912). *Minas Gerais*: Pedra Azul, July 1970, 2♀, 2♂ (F. M. Oliveira, AMNH). *Rio Grande do Sul*: Santa Rosa, 2 Jan. 1984, ♀ (A. D. Brescovit, MCN 11915). PARAGUAY *Caazapá*: Pastoreo, ♀ (D. Wees, MCZ).

Alpaida chapada new species
Figures 97–100; Map 2

Holotype. Female from Chapada dos Guimarães, Est. Mato Grosso, Brazil, 1 Dec. 1983 (M. Hoffmann, MCN no. 11968). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange yellowish, sternum orange. Legs dusky yellowish with narrow black rings at ends of articles and some on middle. Dorsum of abdomen indistinctly banded (Fig. 99); venter with median black patch and white line on each side (Fig. 100). Abdomen elongated, pointed in front and with shoulder humps. Total length 12 mm. Carapace 3.7 mm long, 2.7 wide. First femur 3.2 mm; patella and tibia 4.0; metatarsus 2.8; tarsus 1.0. Second patella and tibia 3.4 mm; third 2.3; fourth 3.6.

Diagnosis. Females differ from most other *Alpaida* species by the shape of the abdomen and from *A. hoffmanni* by the straight longitudinal bands of the abdomen (Fig. 99), and by having the scape of the epigynum more distinctly set off (Figs. 97, 98) and a rounded ridge laterally on the median posterior plate just inside the lip (Fig. 98).

Paratypes. BRAZIL *Pará*: 80 km E Canindé, Rio Maracacume, 22–23 May 1963, ♀ (B. Malkin AMNH). *Mato Grosso*: Chapada dos Guimarães, Nov. 1963, 3♀ (M. Alvarenga, AMNH, MCZ).

Alpaida constant new species
Figures 101, 102; Map 2

Holotype. Male from Benjamin Constant vicinity, Est. Amazonas, Brazil, 18 Sept. 1962 (W. L. Brown, ex MCZ, MZSP). The specific name is a noun in apposition after the locality.

Description. Male. Carapace orange-yellow, eye area, rim dusky. Labium yellow. Endites dusky. Sternum yellow with median dusky mark. Coxae, legs dusky yellow. Dorsum of abdomen with black marks, some white pigment on shoulders and sides (Fig. 101); venter black with two parallel pigmentless lines. Posterior median eyes 0.8, anterior laterals and posterior laterals 0.6 diameter of anterior median eyes. Second tibiae slightly curved at base, with some macrosetae; third and fourth trochanters with a short macroseta. Abdomen oval. Total length 4.2 mm. Carapace 2.2 mm long, 1.7 wide. First femur 2.5 mm; patella and tibia 2.9; metatarsus 2.1; tarsus 0.9. Second patella and tibia 2.1 mm; third 1.9; fourth 2.7.

Diagnosis. The male is distinguished from others by the large distally facing lobe of the median apophysis (Fig. 102).

Alpaida veniliae (Keyserling)
Figures 103–109; Map 2

Epeira veniliae Keyserling, 1865: 817, pl. 19, fig. 23, ♀, ♂. Seven female and one male syntypes from New Granada [Spanish colony of Colombia and Panama] (BMNH), examined. Keyserling, 1893: 256, pl. 13, fig. 191, ♀, ♂.

Epeira pantherina Taczanowski, 1872: 132. Male lectotype here designated from Uassa [Uaça, Amapá, Brazil] (PAN), examined. NEW SYNONYMY.

Epeira unguiformis Keyserling, 1893: 237, pl. 11, fig. 177, ♀. Female from Rio Grande do Sul, Brazil (BMNH), examined. NEW SYNONYMY.

Araneus borellii Simon, 1897c: 6. Female from San Pablo, Prov. Tucumán, Argentina (MZUT), ex-

amined. Tullgren, 1905: 32, pl. 4, fig. 10, ♀, ♂. NEW SYNONYMY.
Araneus veniliae:—F. P.-Cambridge, 1904: 516, pl. 49, figs. 23–24, ♀, ♂. Bonnet, 1955: 627.
Aranea borellii:—Roewer, 1942: 849.
Aranea veniliae:—Roewer, 1942: 859.
Araneus pantherina:—Bonnet, 1955: 562.
Araneus unguiformis:—Roewer, 1942: 855. Bonnet, 1955: 626.
Subaraneus veniliae:—Caporiacco, 1948: 662.
Lariniacantha veniliae:—Archer, 1951: 15.
Metepeira wiedenmeyeri Schenkel, 1953: 22, fig. 20. Male holotype from Pozón, [Falcon] Venezuela (NMB), examined. Brignoli, 1983: 276. NEW SYNONYMY.
Neoscona borellii:—Bonnet, 1958: 3057.
Metazygia unguiformes:—Valle and Valle, 1972: 33.

Description. Female from Panama. Carapace, sternum orange. Legs orange with narrow black rings. Dorsum of abdomen with three white lines and paired black spots (Fig. 106); venter black with white line on each side (Fig. 107). Living specimens have white stripe bordered by red. Carapace slightly pubescent. Abdomen oval, pointed behind, slightly pubescent. Total length 8.6 mm. Carapace 3.6 mm long, 2.8 wide. First femur 3.4 mm; patella and tibia 4.3; metatarsus 3.1; tarsus 1.3. Second patella and tibia 3.6 mm; third 2.5; fourth 3.8.

Male from Panama. Coloration as in female (Fig. 108). Legs with strong macrosetae, one short one under second femora, five to seven under third and fourth femora; second tibiae slightly swollen. Total length 7.4 mm. Carapace 3.9 mm long, 3.1 wide. First femur 3.8 mm; patella and tibia 4.5; metatarsus 4.5; tarsus 1.5. Second patella and tibia 3.7 mm; third 2.5; fourth 3.8.

Variation. Females' total length varies from 6.3 to 12.9 mm, males from 6.3 to 8.7. The smallest specimens come from Colombia, the largest from eastern Brazil. A photograph of a living juvenile specimen has carapace, legs yellowish, abdomen with dorsal black marks surrounded by red, three yellowish lines and white pubescence.

The specimens described and illustrated are from Panama (MCZ).

Diagnosis. The females are distinguished by the distinct color pattern (Fig. 106) and the convex posterior median plate of the epigynum, which is much longer than wide (Fig. 105). The male is distinguished by the large median apophysis with a distal hook and the series of slats on the tegulum under the terminal apophysis (Fig. 109).

Natural History and Distribution. Alpaida veniliae has been collected as wasp prey in Trinidad and Leticia, Colombia; on *Eichhornia crassipes* in Surinam; sugarcane in Venezuela; swampy pond floating vegetation in Colombia; in tropical dry rain forest at Remedios, Colombia; on swamp plants in Dpto. Loreto, Peru; and orange and coffee plantations in São Paulo, Brazil. Behavior observations are recorded by Valle and Valle (1972): the web is 20 to 40 cm in diameter. Kochalka (in letter) writes that in Paraguay *A. veniliae* is found near water, the web is one meter above the ground. The spider is at its hub at night. The egg-sac is tangled, loosely attached to vegetation. In a rice field in Chigorodó, Colombia, the species was found to prey on Cercopidae, Cicadellidae, Pyralidae and Diptera, and immature Orthoptera (E. J. Urueta, personal communication). It is found from Panama to Argentina (Map 2).

Records. PANAMA *Herrera*: Desierto de Sarigua (MIUP). *Colón*: Santa Rosa (AMNH); Frijoles (MCZ). *Panamá*: Pedro Miguel (MCZ); Barro Colorado Isl. (MCZ). *Darién*: El Real de Santa María (AMNH).

LESSER ANTILLES *Trinidad*: Point Fortin (AMNH); St. Augustine (AMNH). VENEZUELA *Lara*: Barquisimeto (CAS). GUYANA Georgetown (AMNH). SURINAM Brokopondo Lk. (AMNH); Paramaribo (AMNH). FRENCH GUIANA Cayenne (PAN). COLOMBIA *Magdalena*: Isla de Salamanca (AMNH). *Atlantico*: Baranquilla (MNHNP). *Bolívar*: Lago de Ayapel, Río Muñoz (AMNH). *Antioquia*: Chigorodó, 30 m (MCZ); Mutatá (MCZ); Remedios (MCZ). *Chocó*: Río San

Juan, 400 m (MCZ). *Meta*: ca. 15 km SW Puerto López, 200 m (MCZ); 20 km S Porvenir, 170 m (MCZ); Porvenir (MCZ); Carimagua (MCZ). *Amazonas*: Leticia (AMNH); 25 km N of Leticia, 90 m (MCZ). PERU *Loreto*: Río Samiria (AMNH); Iquitos (MCZ); Prov. Alto Amazonas (MCZ). BRAZIL *Roraima*: Ireng River (AMNH). *Amazonas*: Alto Solimões (MCN); Rio Autaź Caprauga (NHRM); Rio Japurá Chicago (NHRM); [?] Lago Baixio (MCZ). *Pará*: Belém (AMNH, MCZ). *Ceará*: Fortaleza (MNRJ). *Pernambuco*: Lago Xidara Capim Flutuante (MNRJ); Igarapeaçu Capim Flutuante (MNRJ); S. Pedro da Aldeia (MNRJ). *Mato Grosso*: Barra do Tapirape (AMNH). *Rio de Janeiro*: Itatiaia (AMNH). *São Paulo*: Jaboticabal (MCZ); São Paulo (MCZ). *Paraná*: Foz do Iguaçu (MCZ, MNRJ). *Santa Catarina*: Corupa (AMNH). *Rio Grande do Sul*: Triunfo (MCN); Novo Hamburgo (MCN); Pelotas (AMNH); Porto Alegre (MCN); Viamão (MCN); Muçum (MCN). PARAGUAY *Paraguarí*: near Ybytymí (MCZ); Parque Nac. Ybyouí (MNHNP). *Alto Paraná*: km 12 de Stroessner (MNHNP). *Amambay*: Parque Nac. Cerro Corá (MNHNP, MCZ). *Caazapá*: Pastoreo (MCZ). BOLIVIA *El Beni*: Espíritu, Yacuma (ZSM). ARGENTINA *Misiones*: Montecarlo (AMNH); Iguazú (MEG); General M. Belgrano (MEG). *Chaco*: Roque Sáenz Peña (MLP); Pto. Aguirre (MACN). *Corrientes*: Corrientes (MACN). *Santa Fé*: Arrufó (MCZ). *Salta*: Laurel de Chicoana (MCZ). *Buenos Aires*: Buenos Aires (MCZ). *Río Negro*: El Bolsón area (AMNH).

Alpaida tabula (Simon), new combination
Figures 110–115; Map 3

Araneus tabula Simon 1895: 815, fig. 867, ♀. Two female syntypes from "Amazonas" (MNHN), examined). Bonnet, 1955: 608.

Araneus multipunctatus Simon; 1895: 815. Female holotype from Rio Salobro, Mato Grosso, [Mato Grosso do Sul, Brazil] (MNHN), examined. Bonnet, 1955: 547. Nomen Nudum.

Aranea tabula:—Roewer, 1942: 853.

Aranea multipunctuta:—Roewer, 1942: 847.

Note. A *nomen nudum* need not be cited. Both Roewer (1942) and Bonnet list *A. multipunctata*, but only Bonnet (1955) indicates that the name lacks description and diagnosis. Specimens from the Paris museum with this name on the label were examined.

Description. Female from Ecuador. Head black; thorax yellow. Chelicera black, distally orange. Sternum, coxae yellow. Second and third femora, tibiae, metatarsi, tarsi black, other femora and all patellae yellow. Dorsum of abdomen yellow with black patches, anterior black (Fig. 112); venter, black with yellow (Fig. 113). Abdomen shield-shaped (Fig. 112). Total length 9.4 mm. Carapace 3.5 mm long, 3.4 wide. First femur 3.4 mm; patella and tibia 4.2; metatarsus 2.7; tarsus 1.1. Second patella and tibia 3.7 mm; third 2.4; fourth 3.6.

Male from Bahia. Coloration as in female. Fourth trochanters with two short macrosetae. Abdomen oval, pointed anteriorly (Fig. 114). Total length 4.8 mm.

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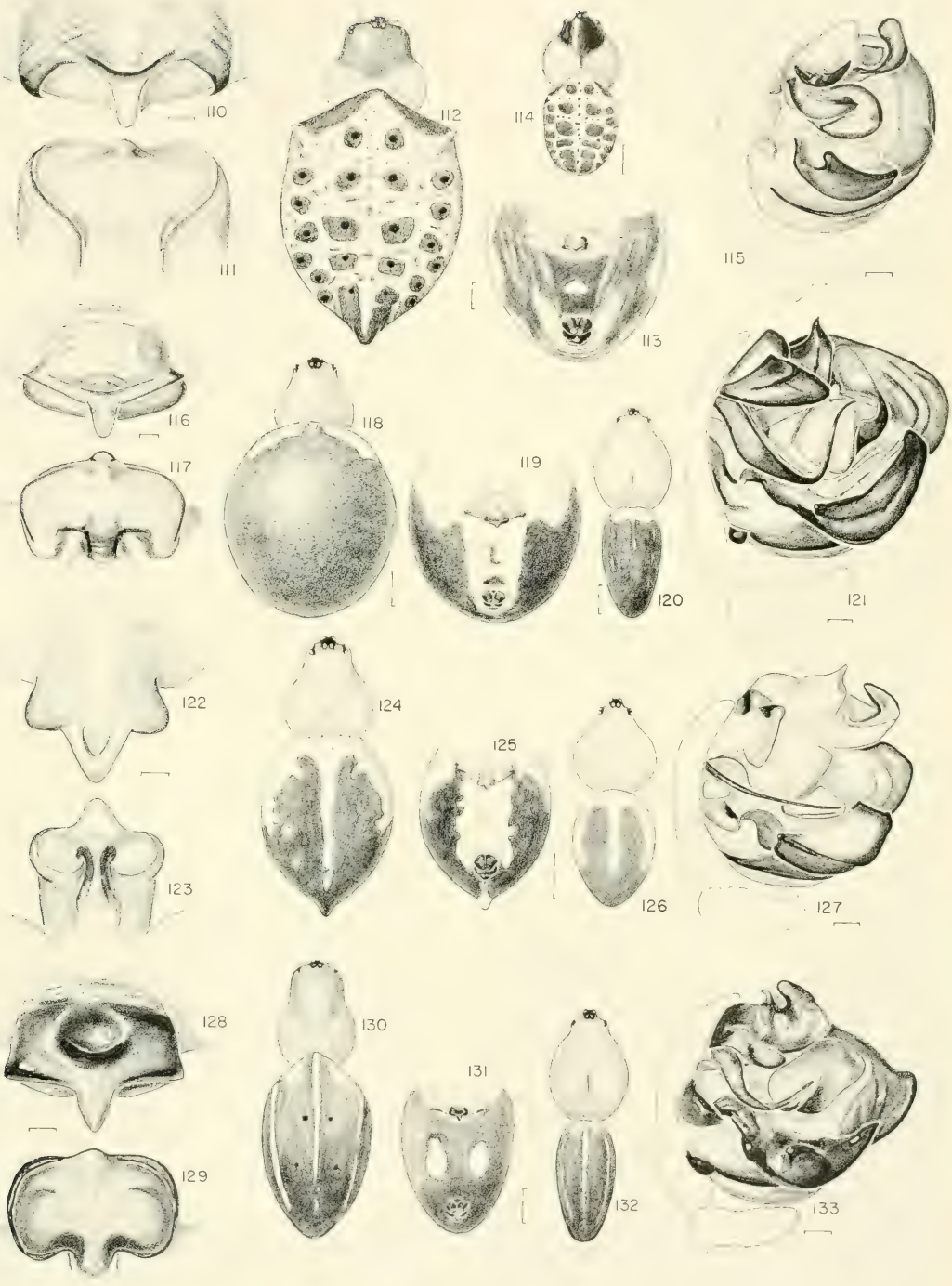
Figures 110–115. *Alpaida tabula* (Simon). 110–113, female. 110, epigynum, ventral. 111, epigynum, posterior. 112, dorsal. 113, ventral. 114, 115, male. 114, dorsal. 115, left palpus.

Figures 116–121. *A. rioja* n. sp. 116–119, female. 116, epigynum, ventral. 117, epigynum, posterior. 118, dorsal. 119, ventral. 120, 121, male. 120, dorsal. 121, palpus.

Figures 122–127. *A. carminea* (Taczanowski). 122–125, female. 122, epigynum, ventral. 123, epigynum, posterior. 124, dorsal. 125, ventral. 126, 127, male.126, dorsal. 127, palpus.

Figures 128–133. *A. alvarengai* n. sp. 128–131, female. 128, epigynum, ventral. 129, epigynum, posterior. 130, dorsal. 131, ventral. 132, 133, male. 132, dorsal. 133, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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Carapace 2.7 mm long, 2.2 wide. First femur 2.7 mm; patella and tibia 3.4; metatarsus 2.1; tarsus 1.1. Second patella and tibia 2.7 mm; third 1.7; fourth 2.5.

Variation. Total length of females 9.2 to 10.0 mm. The syntype female and a male from Bahia (MCN) are described and illustrated.

Diagnosis. In both sexes, the color and form of the abdomen (Figs. 112–114) are more distinctive than the genitalia.

Records. GUYANA *Essequibo*: near Mazaruni Hd., Pakaraima Mts., ♀ (Myers, AMNH). ECUADOR *Napo*: "Napo," May 1946, ♀ (Willina, MACN). PERU *Junín*: Pumamarca, 1,900 m, ♀ (K. Jelski, J. Sztolcman, PAN). BRAZIL *Bahia*: Fazenda Santa Antonio, Uruçuca, 24 Oct. 1978, ♂ (J. S. Santos, MCN 10165). BOLIVIA *La Paz*: Nigrillani, ♀ (W. Willines, MLP).

Alpaida rioja new species
Figures 116–121; Map 2

Holotype. Male from Ilias (?), Prov. La Rioja, Argentina, 1948 (P. M. Gomez, MACN no. 8451). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange. Sternum light orange with some white pigment spots. Coxae light orange; legs black. Dorsum of abdomen black except shoulders orange-white (Fig. 118); venter orange-white, sides black (Fig. 119). Secondary eyes slightly smaller than anterior medians. Fourth legs slightly longer than first. Abdomen oval, almost spherical. Total length 7.9 mm. Carapace 2.6 mm long, 2.3 wide. First femur 2.0 mm; patella and tibia 2.7; metatarsus 1.5; tarsus 0.8. Second patella and tibia 2.3 mm; third 1.6; fourth 2.7.

Male. Coloration as in female except for white streaks on the dorsum of the abdomen (Fig. 120). Total length 6.8 mm. Carapace 3.5 mm long, 2.5 wide. First femur 2.8 mm; patella and tibia 3.6; metatarsus 2.2; tarsus 0.9. Second patella and tibia 2.8 mm; third 2.0; fourth 3.2.

Variation. Total length of females 7.8 to 8.9 mm. One female had broken white streaks on the abdomen as in males (Fig. 120), and a black patch on venter with two white longitudinal bands.

Diagnosis. Females differ from *A. carminea* by having a short, wide epigynum (Fig. 116) and, in posterior view, a median plate with two dorsal lobes (Fig. 117). Males distinguished from *A. carminea* by a longer median apophysis and a long looping embolus in the palpus (Fig. 121).

Paratypes. BRAZIL *Minas Gerais*: Poços de Caldas, fall 1943. ♀ (F. Pough, AMNH). ARGENTINA *La Rioja*: Cuesta de Miranda, Jan. 1964, ♀ (M. E. Galiano, MACN). *Córdoba*: Valle Hermoso, Feb. 1958, ♀ (O. de Ferrariis, AMNH).

Alpaida carminea (Taczanowski), new combination
Figures 122–127; Map 2

Epeira carminea Taczanowski, 1878: 163, pl. 2, fig. 14. Several female syntypes from Amable María, [Dpto. Junín], Peru (PAN), examined.
Epeira deliciosa Keyserling, 1893: 234, pl. 11, fig. 174. Female, male syntypes from Serra Vermelha, Fazenda Calvaria [Est. Rio de Janeiro], Brazil (BMNH) lost. NEW SYNONYMY.
Aranea carminea:—Roewer, 1942: 838.
Aranea deliciosa:—Roewer, 1942; 841.
Araneus carmineus:—Bonnet, 1955: 452.
Araneus deliciosus:—Bonnet, 1955; 485.

Description. Female from Paraguayan Chaco. Carapace, sternum, coxae orange. Labium, endites, legs black. Dorsum of abdomen black with median longitudinal and lateral light bands (Fig. 124); venter with wide, median, longitudinal band, sides black, white under posterior point (Fig. 125). Fourth legs slightly longer than first. Abdomen oval, pointed posterior. Total length 6.7 mm. Carapace 2.7 mm long, 2.1 wide. First femur 2.3 mm; patella and tibia 2.9; metatarsus 1.9; tarsus 0.9. Second patella and tibia 2.5 mm; third 1.8; fourth 3.0.

Male. Coloration as in female (Fig. 126). Total length 5.0 mm. Carapace 2.7 mm long, 1.9 wide. First femur 2.5 mm; patella

and tibia 2.8; metatarsus 1.9; tarsus 0.9. Second patella and tibia 2.3 mm; third 1.7; fourth 2.7.

Note. Both Keyserling and Taczanowski describe the carapace as being crimson.

Variation. Total length of females from 5.0 to 9.1 mm, males from 4.9 to 5.3. Some females have a black patch on the venter of the abdomen surrounded by white.

The female described and illustrated is a syntype of *deliciosa*, the male is from Misiones, Argentina (MACN).

Diagnosis. The abdomen of the female has a characteristic color pattern (Figs. 124, 125) and the epigynum differs from related species by being slightly longer than wide in posterior view (Fig. 123) and having well-set off lateral lobes subequal to the median lobe in ventral view (Fig. 122). The male palpus has a long, slightly curved, saber-shaped embolus and very large terminal apophysis (Fig. 127).

Natural History. Kochalka's notes (in letter) say that the living spider is brilliant red and black. It is found under rocks, logs, boards and trash in disturbed habitats. The tiny web is about 5 cm above the ground out in the open or under an object. Once he observed a female on a brick wall 1.5 m above the ground, near a tangled yellowish egg-sac suspended from a horizontal silk thread.

Records. PERU *Cajamarca*: Alsur de Jaén (AMNH). *Junín*: La Merced (MNRJ); San Ramón (AMNH, MCZ). *Madre dos Dios*: Puerto Maldonado, 300 m (AMNH); Iberia, 150 m (AMNH). BRAZIL *Amazonas*: Manaus (MEG, MZSP, NHRM); Rio Puraquequara (MZSP); Tabatinga (MNRJ); Estrada do Marran, Rio Branco (MZSP). *Mato Grosso do Sul*: Três Lagoas (MZSP); Salobro (MNRJ). *Minas Gerais*: Carmo do Rio Claro (MNRJ); Serinha Minas Diamantina (AMNH); Diamantina (AMNH). *Rio de Janeiro*: S. Antônio do Imbé (AMNH). *São Paulo*: Rio Claro; Amparo (MZSP); Nova Europa (MZSP). *Paraná*: Serrinha (MZSP). PARAGUAY *Central*: Villeta (MCZ, MNHNP); San Lorenzo (MCZ); Luque (MNHNP). *Paraguarí*: La Colmena (MCZ). *Itapúa*: Pirapó (MNHNP, MCZ). ARGENTINA *Misiones*: [no loc.] (MACN). *La Rioja*: La Rioja (MNRJ). *Córdoba*: Calamuchita (MACN). *Buenos Aires*: La Plata (MLP).

Alpaida alvarengai new species
Figures 128–133; Map 2

Holotype. Female from Chapada dos Guimaraes, Mato Grosso, Brazil, Nov. 1963 (M. Alvarenga, AMNH). The species is named after the collector.

Description. Female. Carapace, labium, sternum, endites orange. Coxae black. Legs ringed black on orange. Dorsum of abdomen black with three white bands, light anteriorly (Fig. 130); venter black with two contrasting white patches (Fig. 131), orange anterior to genital groove. Anterior median eyes their diameter apart; posterior median eyes slightly less than their diameter apart. Fourth legs longer than first. Abdomen oval, elongate. Total length 7.7 mm. Carapace 3.0 mm long, 1.9 wide. First femur 2.1 mm; patella and tibia 2.4; metatarsus 1.9; tarsus 0.8. Second patella and tibia 2.3 mm; third 1.7; fourth 2.7.

Male. Coloration, eye structure as in female (Fig. 132). Second tibiae slightly thicker than first, distal end curved. Abdomen oval. Total length 6.5 mm. Carapace 3.1 mm long, 2.1 wide. First femur 2.5 mm; patella and tibia 3.1; metatarsus 2.1; tarsus 0.9. Second patella and tibia 2.4 mm; third 1.8; fourth 2.7.

Note. Right fourth leg of female regenerated; patella and tibia 2.0 mm. Males and female have been matched by color pattern.

Diagnosis. Females differ from *A. holmbergi* by having the notch on the epigynum anterior to the posterior edge and a narrow scape (Fig. 128). The male has an evenly curved long embolus and the median apophysis has a pointed lobe pointing toward the lateral of the palpus (Fig. 133). Both sexes have a distinct pair

of white patches on the venter of the abdomen (Fig. 131).

Paratype. BRAZIL *Pará*: Aldeia Maracacume, Rio Maracacume, 80 km E of Canindé, 22, 23 May 1963, ♂ (B. Malkin, AMNH).

Alpaida holmbergi new species
Figures 134–137; Map 2

Holotype. Female from Sierra de la Ventana, Prov. Rio de Janeiro, Argentina, 17 Dec. 1971 (M. E. Galiano, MACN no. 8494). The species is named after the first Argentinian arachnologist.

Description. Female. Carapace orange, eye region black. Clypeus, labium, sternum black. Endites, coxae black, fourth coxae orange; legs ringed black and yellow. Dorsum of abdomen black with three white bands (Fig. 136); venter with a pair of white parallel lines on black (Fig. 137). Anterior median eyes slightly more than their diameter apart; posterior median eyes 1.4 diameters apart. Abdomen almost spherical with an anterior median hump. Total length 6.0 mm. Carapace 2.5 mm long, 2.0 wide. First femur 2.0 mm; patella and tibia 2.5; metatarsus 1.6; tarsus 0.7. Second patella and tibia 2.1 mm; third 1.5; fourth 2.2.

Note. Six juvenile specimens of this species from Buenos Aires labeled *Epeira burmeisteri* Holmberg are in the Keyserling collection in the British Museum. But they do not fit Holmberg's description of adult *Epeira burmeisteri*, which is that of an *Eriophora*.

Diagnosis. Females have a dorsal abdomen pattern like *A. alvarengai* and *A. chaco* but the venter has two broken white lines (Fig. 137). The epigynum differs by having the edge of the median lobe gently curved (Fig. 134) and the posterior median plate lobed on each side dorsally (Fig. 135), while in the other two species the median lobe is set off.

Paratypes. ARGENTINA *Neuquen*: San Martín de los Andes, 640 m, 29 Sept. 1981, 3♀ (Nielsen, Karsholt, ZMK).

Alpaida santosi new species
Figures 138, 139; Map 2

Holotype. Male from Fazenda Almada, Uruçuca, Bahia, Brazil, 27 Nov. 1977 (J. S. Santos, MCN no. 10386). The species is named after the collector.

Description. Male. Carapace orange, head dusky. Labium, endites, coxae dusky. Sternum orange. Legs orange-yellow, distal half of femora, patellae and proximal half of tibiae dusky. Dorsum of abdomen with paired and median black patches; sides with longitudinal black band (Fig. 138); venter pigmentless except spinnerets and immediate surrounding area black. Anterior median eyes 0.5 their diameter apart; posterior median eyes 0.6 their diameter apart. Total length 2.1 mm. Carapace 1.2 mm long, 1.0 wide. First femur 1.3 mm; patella and tibia 1.4; metatarsus 0.9; tarsus 0.5. Second patella and tibia 1.2 mm; third 0.9.

Diagnosis. The male differs from other *Alpaida* by the long, wide curved embolus and large folded median apophysis of the palpus (Fig. 139).

Alpaida chaco new species
Figures 140–142; Map 2

Holotype. Female from Parque Nacional Defensores del Chaco, between Picada Vieja and Cabo Cano, 68°5'W, 20°20'S, Dpto. Chaco, Paraguay, 28 Aug. 1982 (J. A. Kochalka, MNHNP). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, coxae orange. Legs with proximal

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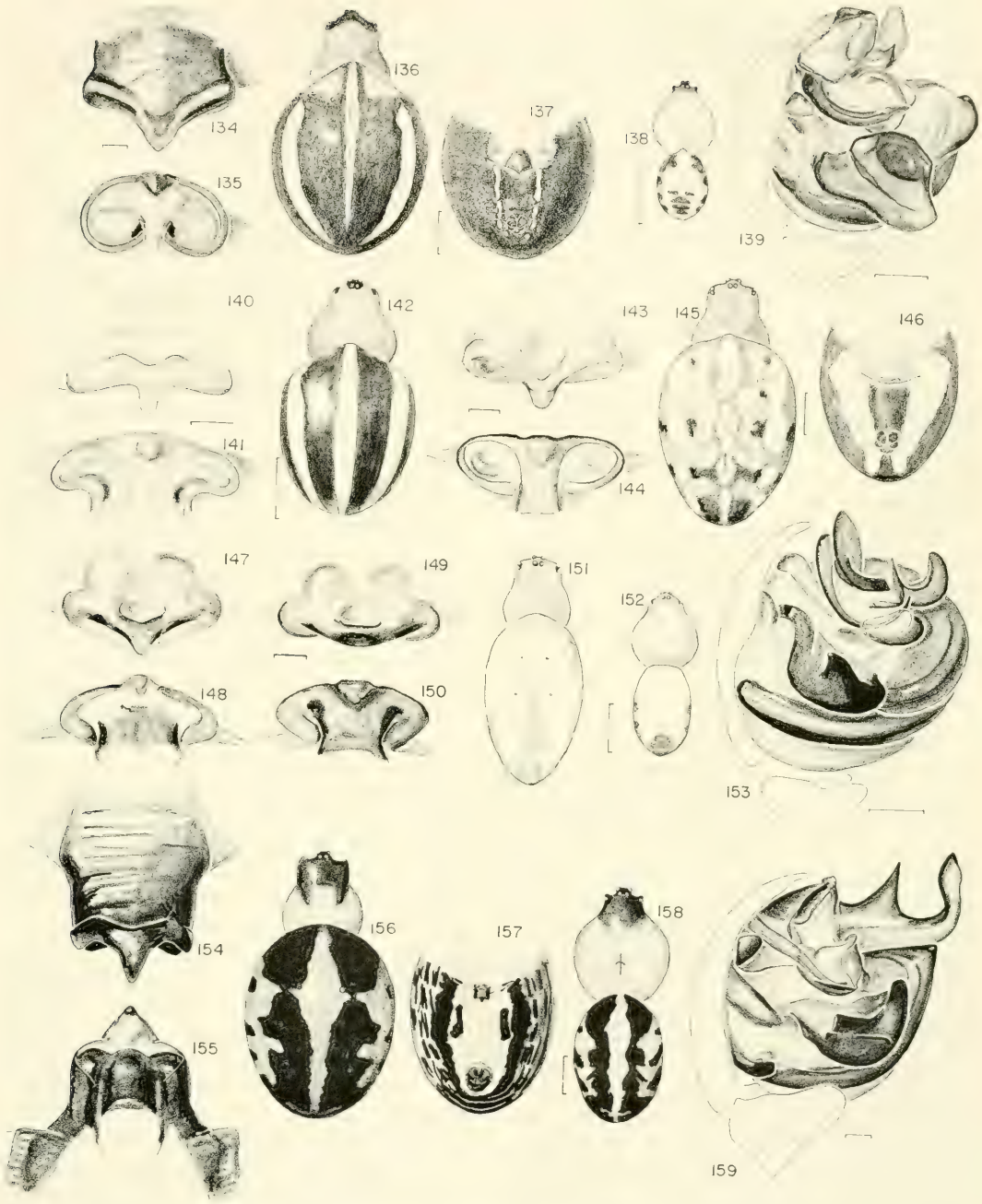
Figures 147–153. *A. dominica* n. sp. 147–152, female. 147–150, epigynum. 147, 149, ventral. 148, posterior. 149, 150, lobe torn off. 151, dorsal. 152, 153, male. 152, dorsal. 153, palpus.

Figures 154–159. *A. versicolor* (Keyserling). 154–157, female. 154, epigynum, ventral. 155, epigynum, dorsal. 156, dorsal. 157, ventral. 158, 159, male. 158, dorsal. 159, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.



Figures 134–137. *Alpaida holmbergi* n. sp., female. 134, epigynum, ventral. 135, epigynum, posterior. 136, dorsal. 137, ventral.

Figures 138, 139. *A. santosi* n. sp., male. 138, dorsal. 139, left palpus.

Figures 140–142. *A. chaco* n. sp., female. 140, epigynum, ventral. 141, epigynum, posterior. 142, dorsal.

Figures 143–146. *A. elegantula* (Archer), female. 143, epigynum, ventral. 144, epigynum, posterior. 145, dorsal. 146, ventral.

half of femora orange, distal half and distal articles black. Dorsum of abdomen black with five white bands (Fig. 142); venter orange, spinnerets black. Eyes subequal in size. Anterior median eyes their diameter apart; posterior medians 0.4 diameter apart. Abdomen oval with a slight median anterior hump (Fig. 142). Total length 3.9 mm. Carapace 1.8 mm long, 1.5 wide. First femur 1.5 mm; patella and tibia 1.8; metatarsus 1.1; and tarsus 0.5. Second patella and tibia 1.5 mm; third 1.0; fourth 1.6.

Diagnosis. The female differs from that of *A. holmbergi* by having the posterior edge of the epigynum straight with a small set-off median lobe and the anterior edge of the lip transverse with a shallow median notch (Fig. 140).

Natural History. Kochalka (in letter) writes that the spider comes from low thorn forest with cacti, usually dry but subject to periodic flooding. It was black and yellow striped with the carapace orange when alive.

Alpaida elegantula (Archer)
Figures 143–146; Map 2

Lariniacantha elegantula Archer, 1966: 132, figs. 8, 9, ♀. Two female syntypes from Sainte Anne, Martinique, Lesser Antilles (AMNH), examined.
Alpaida elegantula:—Brignoli, 1983: 256.

Description. Female. Carapace, sternum, legs yellow. Dorsum of abdomen covered with white pigment spots overlain by two orange bands having dark spots on each side (Fig. 145); venter with median black band, with white pigment on each side having an orange cast (Fig. 146). Anterior median eyes slightly more than their diameter apart; posterior median eyes slightly less than their diameter apart. Abdomen oval [in poor, shriveled condition]. Total length 5.8 mm. Carapace 2.3 mm long, 1.8 wide. First femur 2.1 mm; patella and tibia 2.6; metatarsus 1.7; tarsus 0.8. Second patella and tibia 2.3 mm; third 1.5; fourth 2.3.

Diagnosis. The posterior median plate of the epigynum (Fig. 144) is narrower dorsally than that of *A. dominica*, the abdomen is wider and with more distinct markings (Fig. 145).

Alpaida dominica new species
Figures 147–153; Map 2

Holotype. Female from Dominica, Lesser Antilles, 27–30 Jan. 1968 (B. Malkin, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, legs yellow. Dorsum of abdomen whitish with dusky longitudinal streaks (Fig. 151); venter without pigment. Anterior median eyes slightly more than their diameter apart; posterior median eyes slightly less than their diameter apart. Abdomen rounded anteriorly, pointed behind, with slight shoulder humps (Fig. 151). Total length 4.9 mm. Carapace 2.0 mm long, 1.5 wide. First femur 1.8 mm; patella and tibia 2.1; metatarsus 1.4; tarsus 0.6. Second patella and tibia 1.8 mm; third 1.3; fourth 2.1.

Male. Coloration as in female, but black marks on abdomen more distinct (Fig. 152). Eyes as in female. Second tibiae only slightly thicker than first. Total length 3.4 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.7 mm; patella and tibia 1.8; metatarsus 1.2; tarsus 0.6. Second patella and tibia 1.6 mm; third 1.1; fourth 1.5.

Note. When the white exudate in the epigynum is removed, the tip breaks off and is removed with it (Figs. 149, 150). The male paratype has only a right palpus, Figure 153 is its mirror image.

Variation. Females vary in total length from 4.5 to 5.5 mm. Figures 147, 148 were made from the holotype.

Diagnosis. Females are distinguished from *A. elegantula* by the almost straight posterior edge of the notch of the epigynum (Figs. 147, 149) and the dorsally wide median posterior plate (Figs. 148, 150). The males have a distinctly shaped median apophysis, embolus and tripartite terminal apophysis (Fig. 153).

Paratypes. LESSER ANTILLES *Dominica*: Salibia, 27–30 Jan. 1968, 2♀, ♂ (B. Malkin, AMNH); Portsmouth, July 1979,

2♀ (N. L. H. Krauss, AMNH); Roseau, June 1911, ♀ (AMNH); July 1976, 3♀ (N. L. H. Krauss, AMNH, MCZ). *Montserrat*: Plymouth, Nov. 1967, ♀ (N. L. H. Krauss, AMNH). *Antigua*: St. John's, July 1979, ♀ (N. L. H. Krauss, AMNH).

Alpaida versicolor (Keyserling), new combination
Figures 154–159; Map 3

Cercidia versicolor Keyserling, 1877: 86, pl. 3, fig. 2, ♀. Female holotype from Uruguay (BMNH), examined. Keyserling, 1892: 38, pl. 2, fig. 33, ♀, ♂. Roewer, 1942: 866.
Araneus versicolor:—Bonnet, 1955: 628.

Note. Keyserling (1877) reports on several specimens, one alleged to have come from Madagascar. This may be an error in labeling. Keyserling does not mention this specimen later in 1892 and there is only one holotype.

Description. Female. Carapace and sternum orange; head black. Chelicerae, labium, endites black. Coxae orange with proximal black patch; first two legs mostly black; last two legs broadly but indistinctly ringed black on orange. Abdomen black and light orange (Figs. 156, 157). Carapace with some scattered white hairs. Abdomen oval with some scattered white setae. Total length 7.5 mm. Carapace 3.2 mm long, 2.5 wide. First femur 2.3 mm; patella and tibia 2.9; metatarsus 1.9; tarsus 1.0. Second patella and tibia 2.5 mm; third 1.9; fourth 2.9.

Male. Coloration as in female (Fig. 158). Structure as in female, except abdomen oval. Total length 6.0 mm. Carapace 2.9 mm long, 2.5 wide. First femur 2.4 mm; patella and tibia 2.7; metatarsus 2.0; tarsus 1.0. Second patella and tibia 2.4 mm; third 1.9; fourth 2.7.

Variation. Total length of female varies from 5.6 to 9.1 mm, males from 4.9 to 5.8. The descriptions and illustrations are of specimens from Argentina (MCZ).

Diagnosis. Females, like those of *A. carminea*, have the epigynum in posterior view as long as wide (Fig. 155), but differ in having a distinct transverse lip in ventral view and lack the notch on the median lobe (Fig. 154). The male differs from *A. carminea* by having a shorter thicker embolus in the palpus, a distal lobe on the median apophysis, and the two tips of the terminal apophysis longer (Fig. 159).

Natural History. In two records from Argentina, this species was collected in a pasture.

Records. BRAZIL *Rio Grande do Sul*: Gramado (MCN 1560); Júlio de Castiehos (MCN); Torres (MCN); Porto Alegre (MCN); Capão da Canoa (MACN). URUGUAY *Montevideo*: Montevideo (MNRJ, MZK). *Artigas*: Arroyo Cuaro (MHNM); Tres Cruces (MHNM). PARAGUAY *Guairá*: Colonia Independencia (MNHNP). BOLIVIA *Potosí*: 45 km W Ravelo (AMNH). ARGENTINA *Misiones*: Pto. Casado Chaco Papaguayo (MACN). *Salta*: Pampa Grande (AMNH, MCZ). *Chaco*: Roque Sáenz Peña (MACN, MLP). *Santiago del Estero*: Santiago del Estero (MNRJ); Sumampa (MLP); 70 km W Santiago (MCZ). *Tucumán*: Tafí del Valle, 2,000 m (MCZ). *La Rioja*: Patquía (MEG). *Mendoza*: [?] Canigal (MACN). *Santa Fé*: Delta de Paraná Río Caraguatay (MACN); Santa Fé, Rosario (ZMK); Cruz Alta (ZMK); Carcarañá (MLP). *Entre Ríos*: Paranacito (MACN); San Feliciano (MACN); Concepción del Uruguay (MLP). *San Luis*: San Luis (MLP). *Córdoba*: Calamuchica (MACN); Agua de Oro (MACN); Bajo Grande (MLP); Jesús María (MLP); Cordoba (MCZ); Manfredi (MCZ); Nono (MCZ). *Buenos Aires*: Buenos Aires (MACN, ZMK); Paraná de las Palmas (MEG); Boulogne (MLP); Haedo (MLP); Arrecifes (MLP); Rojas (MNRJ). *La Pampa*: Realico (MACN). *Río Negro*: Viedma (MACN).

Alpaida vanzolinii new species
Figures 160–165; Map 3

Holotype. Female from Caraguatatuba (Massaguaçu), Est. São Paulo, Brazil, 14 July 1964, ♀ (Expedition Dept. Zool., MZSP no. 6214). The species is named after P. Vanzolini, the director of the São Paulo museum.

Description. Female. Carapace dusky orange. Sternum orange. Legs dusky orange. Dorsum of abdomen with indistinct median and paired dusky patches, posterior tip black, lateral white patches connect anteriorly by a white line (Figs. 162, 163) venter without marks, spinnerets black. Posterior median eyes twice the diameter of others. Anterior median eyes their diameter apart; posterior median eyes slightly less than their diameter apart. Legs with many macrosetae; abdomen elongate (Figs. 162, 163). Total length 5.5 mm. Carapace 1.8 mm long, 1.6 wide. First femur 2.4 mm; patella and tibia 2.5; metatarsus 1.9; tarsus 0.8. Second patella and tibia 2.1 mm; third 1.3; fourth 2.5.

Male. Carapace yellow with thin median dusky line, otherwise color as in female (Fig. 164). Posterior median eyes 1.5 times diameter of others. Second tibiae thicker than first and with macrosetae. Fourth trochanters and fourth coxae each with a short macroseta. Total length 3.8 mm. Carapace 1.6 mm long, 1.4 wide. First femur 2.2 mm; patella and tibia 2.5; metatarsus 1.5; tarsus 0.7. Second patella and tibia 1.6 mm; third 1.2; fourth 2.0.

Variation. Females vary in total length from 5.1 to 5.5 mm. The female holotype and the male from Peru are described and illustrated.

Diagnosis. The female can be separated from other species with an elongate oval abdomen lacking an anterior median hump by the epigynum which has a much longer posterior median plate (Fig. 161) than that of *A. morro* and *A. montecarlo.* The male has a sickle-shaped embolus below a large sclerotized terminal apophysis (Fig. 165).

Paratypes. PERU *Huánuco*: Monzón Valley, Tingo María, 10 Nov. 1954, ♀ (E. S. Ross, E. I. Schlinger, CAS); Tingo María, 10 Jan. 1947, ♂ (J. Pallister, AMNH). BRAZIL *Amazonas*: Fonte Bôa, Sept. 1975, 3♂ (M. Oliveira, AMNH, MCZ). ARGENTINA *Misiones*: Eldorado, 1964, 3♀ (A. Kovacs, AMNH).

Alpaida morro new species
Figures 166–169; Map 3

Holotype. Female from Santa Isabel do Morro, Ilha do Bananal, Goiás, Brazil, June 1961 (M. Alvarenga, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellowish orange with a median dusky longitudinal patch and dusky line on thoracic edge. Sternum, legs yellow-orange. Dorsum of abdomen white with paired dusky to black patches (Fig. 168); sides with a black and dusky line bordered above by the dorsal white; venter with a longitudinal dusky rectangle on gray, spinnerets black (Fig. 169). Anterior median eyes and posterior medians each their diameter apart. Abdomen rounded in front and behind. Total length 4.3 mm. Carapace 1.5 mm long, 1.2 wide. First femur 1.5 mm; patella and tibia 1.7; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.6 mm; third 1.0; fourth 1.6.

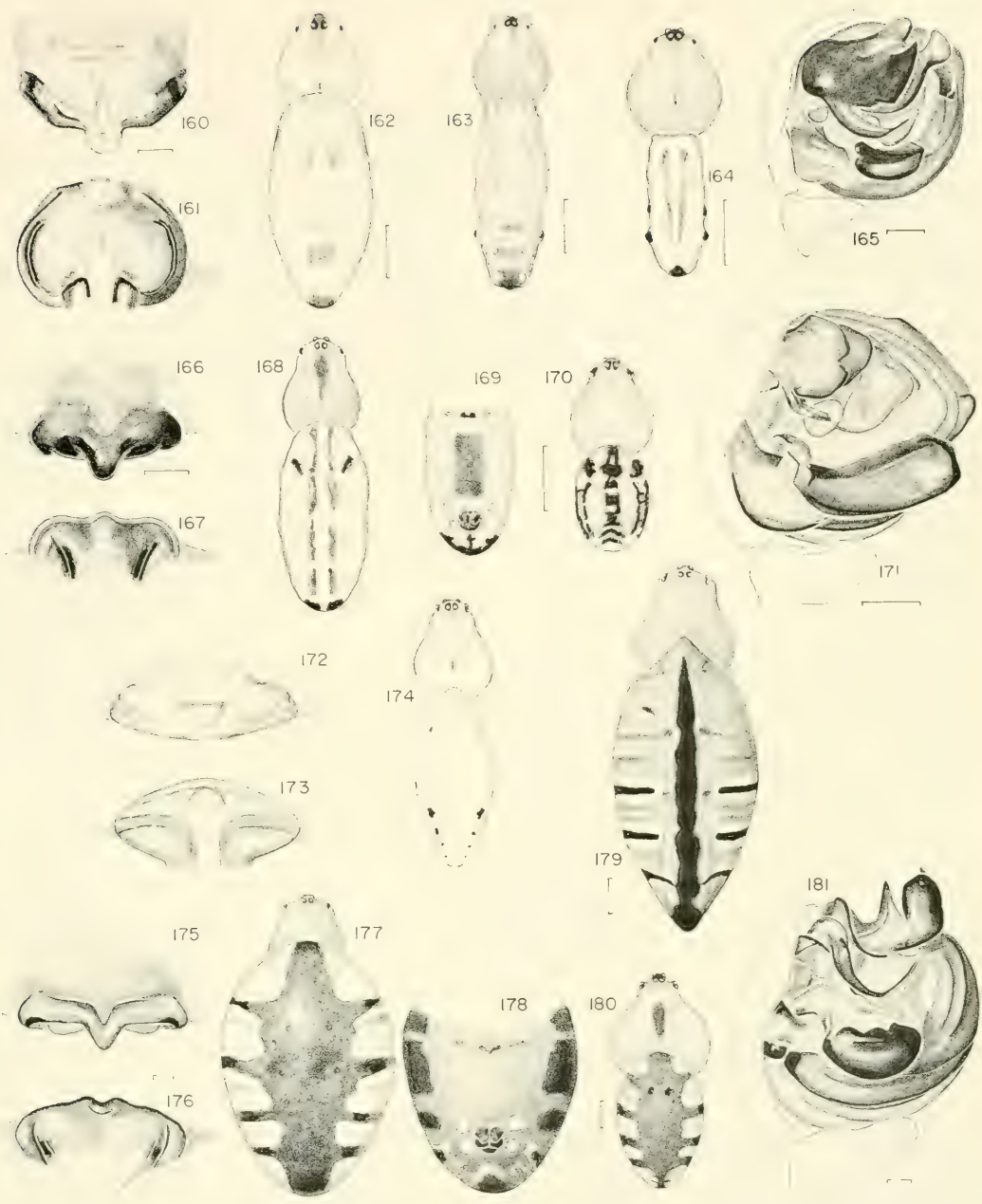
Diagnosis. This female is distinguished from *A. vanzolinii* by the distinct notch in the epigynum (Fig. 166) and, in posterior view, by the dorso-ventrally shorter median plate (Fig. 167).

Alpaida lanei new species
Figures 170, 171; Map 3

Holotype. Male from Honto Florestal, Capital, São Paulo, Brazil, 2 Dec. 1943 (F. Lane, MZSP no. 4547). The species is named after the collector.

Description. Male. Carapace, sternum, coxae yellow. Legs yellowish, distal articles with indistinct dusky rings. Dorsum of abdomen with three longitudinal black bands each enclosing some white pigment spots; venter with a few widely scattered white pigment spots. Total length 2.9 mm. Carapace 1.5 mm long, 1.2 wide. First femur 1.5 mm; patella and tibia 1.7; metatarsus 0.9; tarsus 0.5. Second patella and tibia 1.3 mm; third 0.9; fourth 1.3.

Variation. Total length of males varies from 2.8 to 2.9 mm. The median dorsal



Figures 160–165. *Alpaida vanzolinii* n. sp. 160–163, female. 160, epigynum, ventral. 161, epigynum, posterior. 162, 163, dorsal. 162, (São Paulo, Brazil). 163, (Prov. Misiones, Argentina). 164, 165, male. 164, dorsal. 165, left palpus.

Figures 166–169. *A. morro* n. sp., female. 166, epigynum, ventral. 167, epigynum, posterior. 168, dorsal. 169, ventral.

Figures 170, 171. *A. lanei* n. sp., male. 170, dorsal. 171, palpus.

Figures 172–174. *A. montecarlo* n. sp., female. 172, epigynum, ventral. 173, epigynum, posterior. 174, dorsal.

Figures 175–181. *Alpaida latro* (Fabricius). 175–178, female. 175, epigynum, ventral. 176, epigynum, dorsal. 177, dorsal. 178, ventral. 179, immature. 180, 181, male. 180, dorsal. 181, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

area of the abdomen lacks marks in the paratype.

The male holotype is described and illustrated.

Diagnosis. The male is separated from others by the long rectangular median apophysis with a lobe directed toward the cymbium and the squarish terminal apophysis of the palpus (Fig. 171).

Paratype. ARGENTINA *Misiones*: Gral. Manuel Belgrano, Jan. 1966, ♂ (M. E. Galiano, MACN 8449).

Alpaida montecarlo new species
Figures 172–174; Map 3

Holotype. Female from Montecarlo, Prov. Misiones, Argentina, Jan. 1966 (M. E. Galiano, MACN no. 8473). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellowish. Sternum, legs yellow. Dorsum of abdomen white with pairs of black spots (Fig. 174); venter yellowish. Posterior median eyes 1.8 diameters; anterior laterals and posterior laterals 0.8 diameter of anterior median eyes. Anterior median eyes 1.6 diameters apart, 1.5 diameters from laterals. Posterior median eyes slightly less than their diameter apart, 1.3 diameters from laterals. Second legs longer than fourth. Abdomen elongate (Fig. 174). Total length 4.0 mm. Carapace 1.6 mm long, 1.3 wide. First femur 2.1 mm; patella and tibia 2.9; metatarsus 2.4; tarsus 0.9. Second patella and tibia 2.5 mm; third 1.3; fourth 2.3.

Variation. Females vary in total length from 4.0 to 4.9 mm.

Diagnosis. The female is distinguished from *A. morro* and *A. vanzolinii* by the absence of a posterior median lobe on the epigynum and by the straight posterior edge of the notch (Fig. 172). The lobe might have been torn off when mating.

Note. The generic placement is doubtful. It has a narrower head than other species.

Paratype. ARGENTINA *Río Negro*: El Bolsón area, 1965–1966, ♀ (A. Kovacs, AMNH).

Alpaida latro (Fabricius), new combination
Figures 175–181; Map 3

Aranea latro Fabricius, 1793: 412. Specimen from America (ZMK), lost. Roewer, 1942: 845.
Epeira latro:—Walckenaer, 1841: 113. Keyserling, 1878: 574, pl. 14, fig. 3, ♀. 1892: 197, pl. 9, fig. 146, ♀.
Miranda latro:—C. L. Koch, 1845: 158, fig. 933.
Lariniacantha latro:—Archer, 1951: 15.
Araneus latro:—Bonnet, 1955: 527.

Note. This species was first illustrated by C. L. Koch. I am following Koch and Keyserling in using the name *latro* for this species.

Description. Female. Carapace, sternum, coxae orange. Legs black. Dorsum of abdomen black with lateral light patches enclosing dark transverse stripes (Fig. 177); venter orange; spinnerets, black. Abdomen elongate to oval. Total length 10.5 mm. Carapace 3.7 mm long, 2.8 wide. First femur 3.7 mm; patella and tibia 4.3; metatarsus 3.1; tarsus 1.2. Second patella and tibia 3.6 mm; third 2.5; fourth 4.0.

Male. Coloration as in female (Fig. 180). Second tibiae thicker and with macrosetae. Abdomen oval. Total length 8.7 mm. Carapace 4.4 mm long, 3.6 wide. First femur 4.3 mm; patella and tibia 5.0; metatarsus 3.4; tarsus 1.4. Second patella and tibia 3.9 mm; third 2.7; fourth 4.0.

Variation. The eyes may be on black spots, the carapace may have a black patch (Fig. 180) and there may be more black on the venter. Some females have only the midline of the abdomen black (Fig. 179). Total length of females varies from 8.4 to 12.1 mm, males from 7.5 to 8.3.

The illustrations of the epigynum and Figure 179 are from a specimen from Paraguay (MCZ); Figures 177, 178 from a specimen from Goiás and illustrations of the male from a specimen from Montevideo (MHNM).

Diagnosis. Both males and females are most easily recognized by the unique color markings and shape of the abdomen (Figs. 177–180).

Records. BRAZIL *Pará*: Conceição do Araguaia, July 1959, ♀ (Alvarenga, AMNH). *Goiás*: Corumbá Monjolinha, 6 June 1942, 2 imm. (F. Hana, MZSP 7292); Jaraguá, 12 June 1942, 4♀, 2♂ (F. Lane, MZSP 5159). *São Paulo*: Itapetininga, 13 Sept. 1967, ♂ (E. X. Rabello, MZSP 6823); Ipiranga, imm. (MZSP 7461). *Paraná*: Rio Papagaio Campo Largo, Mar. 1949, ♀ (Gofferge, MZSP 6574). *Rio Grande do Sul*: Bossoroca, 15 Feb. 1972, ♀ (P. C. Braum, MCN); Porto Alegre, 15 Aug. 1968, ♀ (A. A. Lise, MCN), ♀ (R. Buck, MNRJ); Pelotas, Jan. 1958, ♀ (C. Biezanko, AMNH). URUGUAY *Montevideo*: Montevideo, Jan. 1958, 7♀, 2♂ (R. M. Capocasale, MHNM); Malvin, 13 Mar. 1964, ♀ (F. Achaval, MHNM); Puerto Buceo, 21 July 1962, ♀ (R. Capocasale, MHNM); Manga, 3 Nov. 1963, imm. (F. Achaval, MHNM); Isla Buchental, Río Uruguay, 9 Oct. 1963, 2♀ (R. Capocasale, MHNM). *Florida*: Casupa, 4 Dec. 1973, 3♀, ♂ (R. Capocasale, MHNM). *Maldonado*: Piriapolis, 28 June 1953, 2♀, ♂ (Barreiro, MHNM). *Rocha*: La Pedrera, Dec. 1974, ♀ (F. Costa, MHNM). ARGENTINA *Formosa*: Palo Santo, ♀ (H. Hepper, MACN).

Alpaida alticeps (Keyserling), new combination
Figures 182–187; Map 3

Epeira alticeps Keyserling, 1880: 311, pl. 4, fig. 13, ♀. Female holotype from Nova Friburgo, Est. Rio de Janeiro, Brazil (BMNH), examined.

Epeira undulata Bertkau, 1880: 89, pl. 2, fig. 32, ♀. Ten ♀, 3♂ syntypes from Copa Cabana [Rio de Janeiro], Brazil (ZMH), not examined.

Epeira göldii Karsch, 1886: 92, pl. 3, fig. 9, ♀, ♂. Three female, two male, one juv., syntypes from Rio de Janeiro, Brazil (ZMB), examined.

Araneus carteri Badcock, 1932: 25. Penultimate female, penultimate male from Corcovado, Rio de Janeiro, Brazil (BMNH), examined. Bonnet, 1955: 452. NEW SYNONYMY.

Aranea carteri:—Roewer, 1942: 838.

Verrucosa alticeps:—Roewer, 1942: 879.

Araneus alticeps:—Bonnet, 1955: 432.

Description. Female from Rio de Janeiro. Carapace, orange brown with white setae on head. Sternum, coxae orange. Legs contrastingly ringed black on orange. Dorsum of abdomen with paired black patches (Fig. 184); venter with median black patch surrounded by white (Fig. 185). Abdomen with three pairs lateral humps, hairs on sides (Fig. 184). Total length 14.0 mm. Carapace 5.5 mm long, 4.4 wide. First femur 4.7 mm; patella and tibia 6.2; metatarsus 3.8; tarsus 1.5. Second patella and tibia 5.4 mm; third 3.5; fourth 5.4.

Male from Bahia. Color as in female, venter of abdomen all black. Carapace glabrous. Abdomen as in female, but muscle attachment discs sclerotized (Fig. 186). Total length 10.3 mm. Carapace 5.0 mm long, 4.0 wide. First femur 5.1 mm; patella and tibia 6.2; metatarsus 3.6; tarsus 1.6. Second patella and tibia 4.8 mm; third 3.2; fourth 5.0.

Variation. Females vary in length from 8.8 to 17.5 mm, males from 8.2 to 10.7. The size of the lateral humps on the female abdomen varies from barely discernable to distinct humps.

The description and illustrations are of a female from Rio de Janeiro (MCZ) and a male from Bahia (MCN).

Diagnosis. Both sexes can be distinguished from most species of *Alpaida* by the hairs in the head region and on the sides of the abdomen (Figs. 184, 186). The V formed by the smooth lips of the epigynum is more obtuse (Fig. 182) than that of *A. scriba*. The male is distinguished by a long median apophysis, pointed on each end, and the nearly round outline of the terminal apophysis (Fig. 187).

Records. BRAZIL *Bahia*: Itamaraju, 7 Aug. 1978, ♂ (J. S. Santos, MCN). *Minas Gerais*: Santa Rita de Caldas, July 1953, ♀ (MZSP 7653); Rio Matipoó, Aug. 1919, ♀ (MZSP 5771); Serinha Minas Diamantina, ♀ (AMNH). *Rio de Janeiro*: Camorim, ♀ (MNRJ). *São Paulo*: Mogi das Cruzes, 1945, ♀ (MZSP 7931). *Rio Grande do Sul*: Montenegro, 3 Nov. 1977, 3♀ (MCN 7113); General Câmara, 14 Oct. 1982, ♂ (MCN 10805); Tarumã, Viamão, 5 Jan. 1977, ♀ (MCN 5682).

Alpaida scriba (Mello-Leitão), new combination
Figures 188–190; Map 3

Drexilia scriba Mello-Leitão, 1940: 203. Female holotype from Colatina, Espírito Santo, Brazil (MNRJ no. 58296), examined. Brignoli, 1983: 268.

Description. Female. Carapace, sternum, coxae yellow. Legs yellow with indistinct dusky patches. Dorsum of abdomen with indistinct pairs of dusky streaks, posterior tip black, white pigment on anterior quarter, posterior quarter, and along midline; venter without pigment, spinnerets black. Posterior median eyes 0.8, laterals 0.6 diameter of anterior medians. Anterior median eyes 0.8, laterals 0.6 diameter of anterior medians. Anterior median eyes slightly less than and posterior median their diameter apart. Abdomen with indistinct shoulder humps, posterior tip round, sides bulging slightly. Total length 8.5 mm. Carapace 3.4 mm long, 2.7 wide. First femur 3.0 mm; patella and tibia 3.9; metatarsus 2.3; tarsus 1.1. Second patella and tibia 3.2 mm; third 1.9; fourth 3.3

Diagnosis. Females are distinguished from those of *A. alticeps* by the lack of setae on the head and sides of the abdomen, and by the lips of the epigynum, which form a more acutely angled V (Fig. 188).

Records. BRAZIL *São Paulo*: Bateia, 2 Nov. 1949, ♀ (F. Lane, MZSP 6861).

Alpaida kochalkai new species
Figures 191–193; Map 3

Holotype. Female from Loma Cebolleta, ridge trail, 2,500 m, Sierra Nevada de Santa Marta, Dpto. Magdalena, Colombia, 1 March 1975 (J. Kochalka, MCZ). The species is named after the collector.

Description. Female. Carapace, sternum, legs yellow. Dorsum of abdomen greenish white, white pigment spots and four pairs of indistinct tiny black spots (Fig. 193); venter without pigment. Secondary eyes 1.2 diameters of anterior medians. Anterior median eyes 1.3 their diameter apart; posterior median eyes 1.2 their diameter apart. Abdomen oval, pointed behind, indistinctly scalloped on sides (Fig. 193). Total length 5.2 mm. Carapace 1.9 mm long, 1.6 wide. First femur 1.9 mm; patella and tibia 2.2; metatarsus 1.5; tarsus 0.7. Second patella and tibia 1.8; third 1.1; fourth 1.9.

Diagnosis. The epigynum is longer and less sclerotized (Figs. 191, 192) than that of *A. variabilis* and its posterior plate is wider distally than at its base (Fig. 192).

Alpaida iquitos new species
Figures 194–197; Map 3

Holotype. Female holotype and one female paratype from Iquitos, Peru, May 1920 (W. S. Parrish, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, legs orange. Coxae, lighter orange. Dorsum of abdomen with white pigment, posterior tip black (Figs. 196, 197); venter colorless, marked with an indistinct, dusky square; black posterior to spinnerets. Abdomen elongate, widest anterior (Figs. 196, 197). Total length 5.5 mm. Carapace 2.1 mm long, 1.6 wide. First femur 1.9 mm; patella and tibia 2.3; metatarsus 1.5; tarsus

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Figures 182–187. *Alpaida alticeps* (Keyserling). 182–185, female. 182, epigynum, ventral. 183, epigynum, posterior. 184, dorsal. 185, ventral. 186, 187, male. 186, dorsal. 187, left palpus.

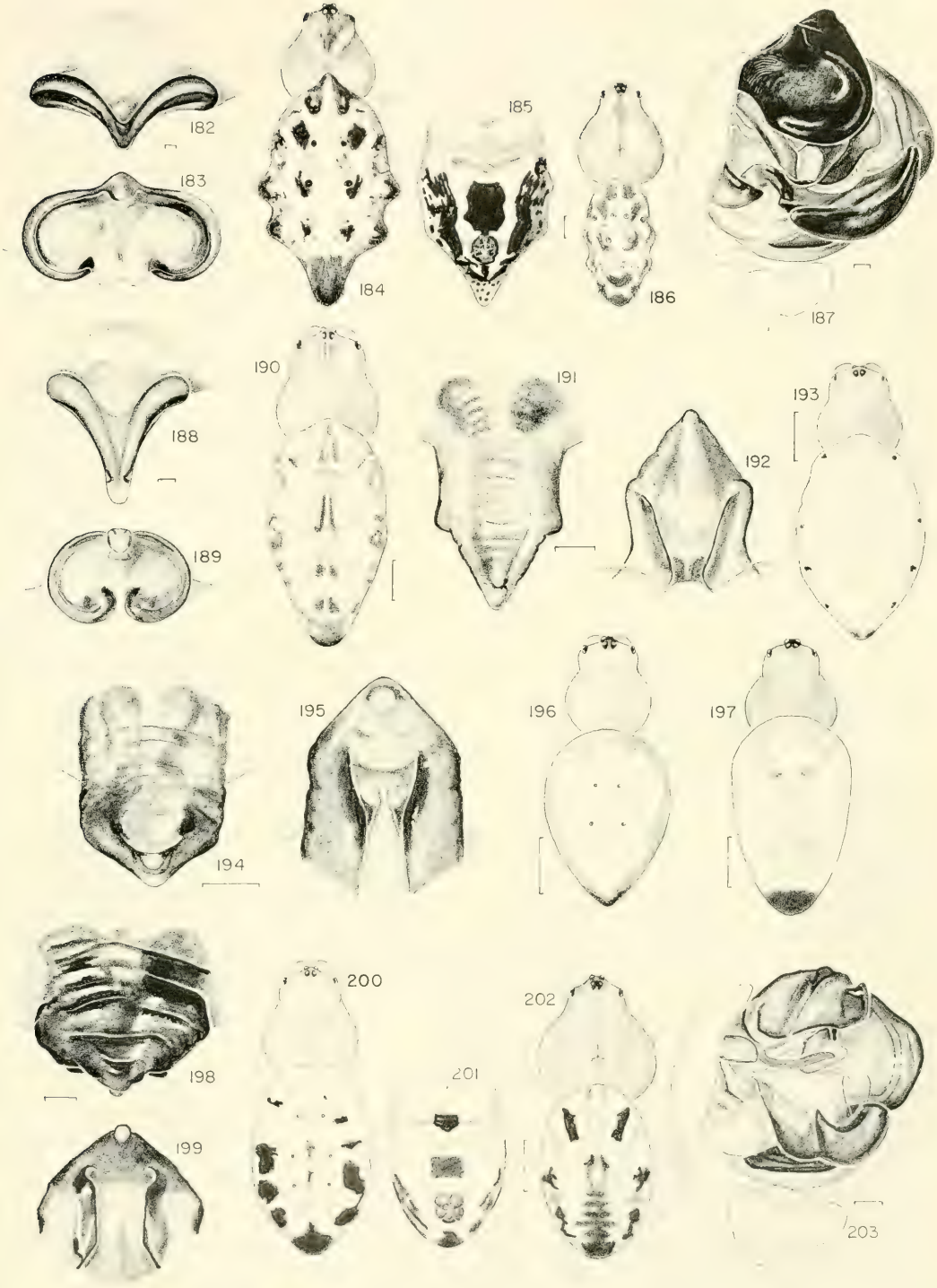
Figures 188–190. *A. scriba* (Mello-Leitão), female. 188, epigynum, ventral. 189, epigynum, posterior. 190, dorsal.

Figures 191–193. *A. kochalkai* n. sp., female. 191, epigynum, ventral. 192, epigynum, posterior. 193, dorsal.

Figures 194–197. *A. iquitos* n. sp., female. 194, epigynum, ventral. 195, epigynum, posterior. 196, 197, dorsal. 196, (Ecuador). 197, (Peru).

Figures 198–203. *A. variabilis* (Keyserling). 198–201, female. 198, epigynum, ventral. 199, epigynum, posterior. 200, dorsal. 201, ventral. 202, 203. male. 202, dorsal. 203, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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0.8. Second patella and tibia 1.9 mm; third 1.2; fourth 1.8.

Variation. Females vary in total length from 4.1 to 5.5 mm. The holotype is illustrated and described.

Diagnosis. Females differ from *A. variabilis* and *A. kochalkai* by having the posterior plate of the epigynum constricted in the middle (Fig. 195) and from *A. variabilis* by having the epigynum longer (Figs. 194, 195).

Paratypes. ECUADOR *Napo*: Río Napo, 2 Jan. 1972, ♀ (Bordon, MACN 8458). BRAZIL *Pará*: Aldeia Coraci 12 km W of Canindé, 16–26 Apr. 1963, ♀ (B. Malkin, AMNH); Canindé, Rio Gurupi, 7–15 Apr. 1963, 7♀ (B. Malkin, AMNH, MCZ, MZSP). *Mato Grosso*: Chapada dos Guimarães, Nov. 1963, ♀ (M. Alvarenga, AMNH).

Alpaida variabilis (Keyserling), new combination
Figures 198–203; Map 3

Araneus variabilis Keyserling, 1864: 126, pl. 6, figs. 1–4, ♀. Several female syntypes from Santa Fé de Bogota, [Bogotá], Colombia (BMNH), examined; 1893: 249, pl. 12, fig. 185, ♀, ♂.
Aranea variabilis:—Roewer, 1942: 855.
Araneus variabilis:—Bonnet, 1955: 627.

Description. Female. Carapace, sternum, legs yellowish. Dorsum of abdomen white with paired black patches, posterior tip black, median area lacking pigment (Fig. 200); posterior half of sides with black marks; venter with a median square black patch (Fig. 201). Abdomen elongate oval. Total length 5.6 mm. Carapace 2.5 mm long, 1.8 wide. First femur 2.0 mm; patella and tibia 2.4; metatarsus 1.5; tarsus 0.7. Second patella and tibia 2.0 mm; third 1.4; fourth 2.0.

Male. Coloration as in female (Fig. 202). Second tibia as thick as first with macrosetae. Abdomen oval. Total length 5.4 mm. Carapace 2.5 mm long, 2.1 wide. First femur 2.3 mm; patella and tibia 2.6; metatarsus 1.5; tarsus 0.7. Second patella and tibia 1.9 mm; third 1.3; fourth 2.0.

Note. A female from Gosomoco (MCZ) and a male from Bogotá (BMNH) are illustrated and described.

Diagnosis. Females differ from *A. kochalkai* and *A. iquitos* by having a more sclerotized, wider epigynum (Figs. 198, 199), with a posterior median plate whose borders are parallel (Fig. 199). The male has a distinctive pointed lobe in the center of the median apophysis and a large, folded over terminal apophysis (Fig. 203).

Records. COLOMBIA Bogotá, 8♂ (BMNH); 16 km W. Bogotá, ♀ (E. I. Schlinger, E. S. Ross, CAS). *Cundinamarca*: Gosomoco [Quebrada Susumuco] 2♀ (E. Reimoser, MCZ).

Alpaida citrina (Keyserling), new combination
Figures 204–206; Map 3

Epeira citrina Keyserling, 1892: 88, pl. 4, fig. 66, ♀. Three female syntypes from Serra Vermelha, Est. Rio de Janeiro, Brazil (BMNH), examined.
Aranea citrinella Roewer, 1942: 839. New name for *Epeira citrina*, since name thought preoccupied by *Aranea citrina* Fourcroy.
Araneus citrinus:—Bonnet, 1955: 461.

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Figures 204–206. *Alpaida citrina* (Simon), female. 204, epigynum, ventral. 205, epigynum, posterior. 206, dorsal.

Figures 207–209. *A. sandrei* (Simon), female. 207, epigynum, ventral. 208, epigynum, posterior. 209, dorsal.

Figures 210–215. *A. manicata* (Simon). 210–213, female. 210, epigynum, ventral. 211, epigynum, posterior. 212, dorsal. 213, lateral. 214, 215, male. 214, dorsal. 215, left palpus.

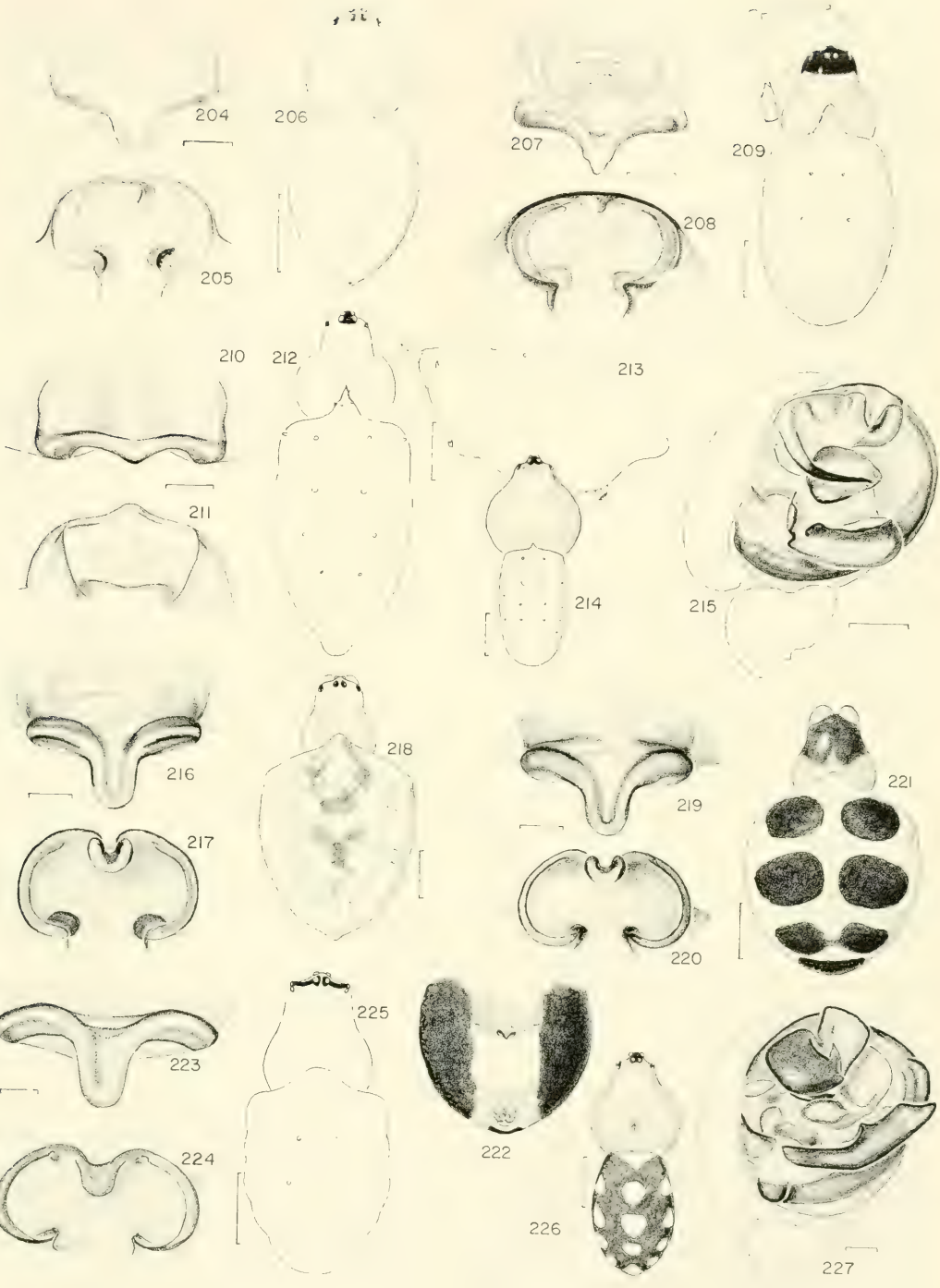
Figures 216–218. *A. canela* n. sp., female. 216, epigynum, ventral. 217, epigynum, posterior. 218, dorsal.

Figures 219–222. *A. lomba* n. sp., female. 219, epigynum, ventral. 220, epigynum, posterior. 221, dorsal. 222, ventral.

Figures 223–225. *A. nigrofrenata* (Simon), female. 223, epigynum, ventral. 224, epigynum, posterior. 225, dorsal.

Figures 226, 227. *A. natal* n. sp., male. 226, dorsal. 227, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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Description. Female. Carapace, sternum yellowish white. Legs yellowish white, with indistinct black rings on distal ends of articles. Dorsum of abdomen white with some dusky pigment posterior; sides white; venter with scattered white pigment spots. Eyes small. Anterior median eyes 1.2 diameters apart; posterior median eyes 1.6 diameters apart. Abdomen with a large anterior median hump (Fig. 206). Total length 3.6 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.6 mm; patella and tibia 1.7; metatarsus 0.9; tarsus 0.5. Second patella and tibia 1.5 mm; third 1.0; fourth 1.4.

Variation. One syntype is 3.4 mm, the other 4.2 in total length; both have three pairs of lateral humps. The total length of other females is intermediate.

A specimen from Rio Grande do Sul is illustrated and described (MCN).

Diagnosis. The shape of the abdomen (Fig. 206), the straight posterior edge of the epigynum (Fig. 204) and the wide lips on each side of the posterior median plate (Fig. 205) separate the species from *A. sandrei.*

Records. BRAZIL *Rio Grande do Sul*: Vila Oliva, Caxias do Sul, 5 Jan. 1976, ♀ (P. A. Buckup, MCN 3944); Linha Alegre, Arroio do Meio, 9 Jan. 1985, ♀ (A. A. Lise, MCN 12901).

Alpaida sandrei (Simon), new combination
Figures 207–209; Map 3

Araneus sandrei Simon, 1895: 816. Female lectotype here designated from Caraça, Minas Gerais, Brazil (MNHN no. 8366), examined. Bonnet, 1955: 589.
Aranea sandrei:—Roewer, 1942: 851.

Note. One paralectotype is similar but has eyes farther apart and the abdomen is shorter; it may be the same species.

Description. Female. Carapace orange, anterior third, including clypeus, black. Chelicerae, sternum, coxae, legs orange. Abdomen orange-white. Anterior median eyes and posterior median eyes 1.3 diameters apart. Abdomen longer than wide, soft with an anterior median projection (Fig. 209). Total length 4.5 mm. Carapace 1.9 mm long, 1.5 wide. First femur 1.6 mm; patella and tibia 1.8; metatarsus 1.2; tarsus 0.6. Second patella and tibia 1.7 mm; third 1.1; fourth 1.6.

Diagnosis. Females are distinguished from those of other species with an anterior median hump on the abdomen by the black head (Fig. 209) and the pointed lobe of the epigynum (Fig. 207).

Alpaida manicata new species
Figures 210–215; Map 3

Araneus manicatus Simon, 1895: 822. Nomen nudum. Bonnet, 1955: 533.
Aranea manicata:—Roewer, 1942: 846.
Holotype. Female from Rio Tocantins [Pará, Brazil] (MNHN no. 606). The specimen had been labeled *manicatus* by Simon.

Note. A juvenile from Tovar labeled *A. manicatus* [Minas Gerais, Brazil] (MNHN 10202) is not this species.

Description. Female. Carapace, sternum, coxae yellow-white. Femora of legs yellow-white, distal articles brownish-black; some articles yellowish-white proximally. Abdomen yellowish-white. Carapace with median eye region projecting. Posterior median eyes 1.2 diameters of anterior medians, laterals about the radius of anterior medians in diameter. Anterior median eyes one diameter apart, posterior medians 1.5 diameters apart. Abdomen longer than wide with an anterior median spine and a pair of small anterior lateral spines (Figs. 212, 213). Total length 5.5 mm. Carapace 1.9 mm long, 1.8 wide. First femur 1.7 mm; patella and tibia 2.0; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.8 mm; third 1.2; fourth 1.8.

Male. Coloration as in female. Eye sizes as in female. Anterior median eyes slightly less than their diameter apart; posterior median eyes their diameter apart. Second tibiae slightly thicker than first with macrosetae. Abdomen oval with a tiny median anterior spine (Fig. 214). Total length 3.1 mm. Carapace 1.6 mm long, 1.4 wide. First femur 1.7 mm; patella and tibia 1.8; meta-

tarsus 1.1; tarsus 0.5. Second patella and tibia 1.4 mm; third 1.1; fourth 1.5.

Note. Males and females were matched because of the anterior spine on the abdomen.

Variation. Females vary in total length from 5.5 to 6.1 mm. Females from Canindé vicinity lack the lateral dorsal spines on the abdomen and have wider abdomens.

The holotype and the male from Canindé (AMNH) are illustrated and described.

Diagnosis. Females differ from *A. citrina* by having the lips of the epigynum in a straight line and only a faint indication of a median lobe (Fig. 210). Males differ from *A. lanei* and others by having an anterior median spine on the abdomen (Fig. 214) and a longer embolus and terminal apophysis (Fig. 215).

Paratypes. BRAZIL *Pará*: 59 km E Canindé, May 1963, ♀ (B. Malkin, AMNH); Canindé, April 1963, ♂ (B. Malkin, AMNH).

Alpaida canela new species
Figures 216–218; Map 3

Holotype. Female holotype and one female paratype from Canela, Rio Grande do Sul, Brazil, 31 Dec. 1973 (A. A. Lise, MCN no. 2055). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, legs light orange. Dorsum of abdomen with white patches all around, some black pigment in middle (Fig. 218); sides white; venter yellowish gray, lacking pigment. Anterior median eyes their diameter apart; posterior median eyes slightly more than their diameter apart. Abdomen shield-shaped with anterior median hump (Fig. 218). Total length 5.5 mm. Carapace 1.8 mm long, 1.4 wide. First femur 1.7 mm; patella and tibia 2.1; metatarsus 1.2; tarsus 0.6. Second patella and tibia 1.8 mm; third 1.1; fourth 1.7.

Diagnosis. Unlike most *Alpaida* the lobe of the epigynum has a deep median groove (Figs. 216, 217). The females differ from *A. lomba* by lacking the contrasting color markings.

Alpaida lomba new species
Figures 219–222; Map 3

Holotype. Female from Morro dos Bois, Lomba Grande, Novo Hamburgo, Rio Grande do Sul, Brazil, 27 Nov. 1980 (A. A. Lise, MCN no. 9418). The specific name is a noun in apposition after the locality.

Description. Female. Carapace light orange, head black. Chelicerae, labium, endites, sternum, palpi, coxae light orange. Femora, patellae, tibiae black; metatarsi, tarsi ringed black on light orange. Dorsum of abdomen white with three pairs of black patches and three posterior black bars (Fig. 221); sides black; venter white between epigynum and spinnerets (Fig. 222). Anterior median eyes 1.4 diameters apart; posterior median eyes slightly more than one diameter apart. Abdomen shield-shaped with anterior median hump. Total length 4.7 mm. Carapace 1.8 mm long, 1.4 wide. First femur 1.3 mm; patella and tibia 1.5; metatarsus 0.9; tarsus 0.5. Second patella and tibia 1.3 mm; third 0.9; fourth 1.4.

Diagnosis. The contrasting markings of the female (Figs. 221, 222) separate this species from others.

Alpaida nigrofrenata (Simon), new combination
Figures 223–225; Map 3

Araneus nigrofrenatus Simon, 1895: 816. Female holotype from Caraça [Minas Gerais], Brazil (MNHN), examined. Bonnet, 1955: 550.

Aranea nigrofrenata:—Roewer, 1942: 848.

Description. Female. Carapace orange, with black band between median and lateral eyes (Fig. 225). Sternum orange. Legs orange with distal half of tibiae black, metatarsi, tarsi black. Abdomen light orange, without marks. Abdomen with anterior hump and paired bulges on sides (Fig. 225). Total length 5.9 mm. Carapace 2.1 mm long, 1.6 wide. First femur 1.7 mm; patella and tibia 2.0; metatarsus 1.1; tarsus 0.6. Second patella and tibia 1.8 mm; third 1.1; fourth 1.7.

Note. The illustrations were made from

the holotype; the description from specimens from Rio Grande do Sul.

Variation. Females vary in total length from 4.5 to 5.9 mm.

Diagnosis. The black band between the eyes (Fig. 225) is diagnostic. The epigynum has a groove in the lobe (Fig. 224), as do several preceding species, but differs by the gentle curvature of the lips on each side of the lobe (Fig. 223).

Records. BRAZIL *Rio Grande do Sul*: Garruchos, São Borja, 8 Dec. 1975, ♀ (A. A. Lise, MCN 3237); Iraí, 20 Nov. 1975, ♀ (MCN 3083).

Alpaida natal new species
Figures 226, 227

Holotype. Male holotype and male paratype from Natal, Rio Grande do Norte, Brazil, June 1911 (Stanford Exped., W. M. Mann, holotype MZSP ex MCZ, paratype MCZ). The specific name is a noun in apposition after the locality.

Description. Male. Carapace, chelicerae, labium, sternum orange. Endites black. Legs dark dusky; coxae dusky yellow, fourth mostly yellow. Dorsum of abdomen black with discrete round white patches (Fig. 226); sides black; venter white with distinct straight border toward black sides, spinnerets dusky. Posterior median eyes 0.8 diameter, lateral eyes 0.7 diameter of anterior median eyes. Total length 4.5 mm. Carapace 2.1 mm long, 1.6 wide. First femur 1.9 mm; patella and tibia 2.2; metatarsus 1.4; tarsus 0.7. Second patella and tibia 1.8 mm; third 1.3; fourth 2.1.

Diagnosis. The contrasting markings of the abdomen (Fig. 226) and the elongate median apophysis with a proximal elongation (Fig. 227) separate this species from others.

Alpaida mato new species
Figures 228–230; Map 3

Holotype: Female from 260 km N of Xavantina, 12°49'S, 51°46'W, 400 m, Est. Mato Grosso, Brazil, cerrado scrub (Xavantina-Cachimbo Exped., ex MCZ, MZSP). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, coxae, proximal quarter of femora, light orange; distal leg articles black. Dorsum of abdomen orange-white with tiny white spots most dense in a longitudinal line (Fig. 230); venter orange-white, spinnerets dark. Secondary eyes 0.8 diameter of anterior medians. Total length 3.2 mm. Carapace 1.2 mm long, 1.0 wide. First femur 1.1 mm; patella and tibia 1.4; metatarsus 0.9; tarsus 0.5. Second patella and tibia 1.2 mm; third 0.8; fourth 1.3.

Diagnosis: The subspherical abdomen (Fig. 230) is unusual in *Alpaida* species. The epigynum lacks the groove on the lobe present in *A. nigrofrenata*, has a transverse black line on the lips (Fig. 228) and has a short wide posterior plate (Fig. 229).

Alpaida biasii new species
Figures 231–233; Map 3

Holotype. Female from Boracéia, Est. São Paulo, Brazil, 28 Feb. 1967 (P. Biasi, MZSP no. 5987). The species is named after the collector.

Description. Female. Carapace dark dusky. Chelicerae dusky. Labium, ster-

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Figures 228–230. *Alpaida mato* n. sp., female. 228, epigynum, ventral. 229, epigynum, posterior. 230, dorsal.

Figures 231–233. *A. biasii* n. sp., female. 231, epigynum, ventral. 232, epigynum, posterior. 233, dorsal.

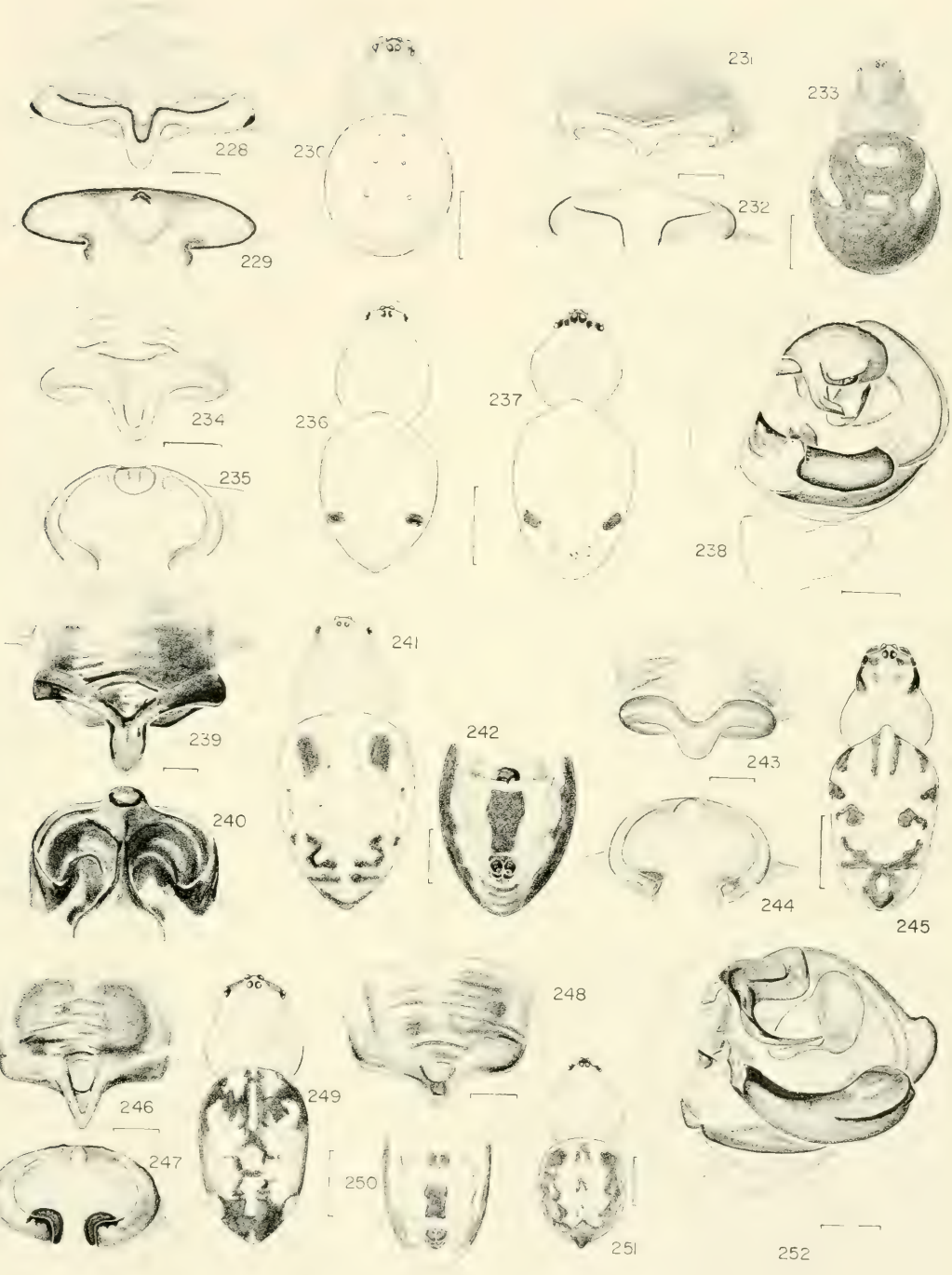
Figures 234–238. *A. bischoffi* n. sp. 234–236, female. 234, epigynum, ventral. 235, epigynum, posterior. 236, dorsal. 237, 238, male. 237, dorsal. 238, left palpus.

Figures 239–242. *A. orgaos* n. sp., female. 239, epigynum, ventral. 240, epigynum, posterior. 241, dorsal. 242, ventral.

Figures 243–245. *A. sumare* n. sp., female. 243, epigynum, ventral. 244, epigynum, posterior. 245, dorsal.

Figures 246–252. *A. pedro* n. sp. 246–250, female. 246, 248, epigynum, ventral. 247, epigynum, posterior. 249, dorsal. 250, ventral. 251, 252, male. 251, dorsal. 252, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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num, endites black. Coxae, legs yellowish-white. Dorsum of abdomen black and white (Fig. 233); venter black with a white spot on each side of spinnerets. Eyes small. Anterior median eyes, posterior median eyes each twice their diameters apart. Abdomen subspherical (Fig. 233). Total length 2.6 mm. Carapace 1.1 mm long, 1.0 wide. First femur 1.2 mm; patella and tibia 1.3; metatarsus 0.8; tarsus 0.5. Second patella and tibia 1.0 mm; third 0.8; fourth 1.1.

Diagnosis. The subspherical abdomen is like that of *A. mato*, but is distinguished by the contrasting color pattern (Fig. 233) and smaller scape of the epigynum (Figs. 231, 232).

Alpaida bischoffi new species
Figures 234–238; Map 3

Holotype. Female from Farroupilha, Rio Grande do Sul, Brazil, 29 Sept. 1978 (N. Bischoff, MCN no. 8318). The species is named after the collector.

Description. Female. Carapace, sternum, legs yellowish-white. Dorsum of abdomen white with a pair of lateral black marks (Fig. 236), dusky transverse marks posteriorly; sides light dusky; venter with scattered white spots, spinnerets dusky. Eyes small, subequal in size. Anterior median eyes and posterior median eyes 1.5 their diameter apart. Abdomen with indistinct shoulder humps and pointed posteriorly (Fig. 236). Total length 3.3 mm. Carapace 1.5 mm long, 1.1 wide. First femur 1.4 mm; patella and tibia 1.5; metatarsus 0.9; tarsus 0.5. Second patella and tibia 1.3 mm; third 1.1; fourth 1.3.

Male. Carapace yellowish-white with a black spot between posterior median and posterior lateral eyes and white pigment spot on thorax. Labium posteriorly black, endites laterally black. Sternum black with median light yellow line. Anterior coxae light, posterior coxae black; legs contrastingly ringed with black. Dorsum of abdomen white with a black spot posteriorly on each side (Fig. 237); venter with black band, widest anteriorly, around pedicel, narrow in front of spinnerets, surrounding spinnerets, longitudinal black lines to side of band. Spinnerets black. Abdomen with slight anterior median hump, slight humps behind black patches (Fig. 237). Total length 3.5 mm. Carapace 1.4 mm long, 1.2 wide. First femur 1.4 mm; patella and tibia 1.5; metatarsus 0.8; tarsus 0.5. Second patella and tibia 1.3 mm; third 0.8; fourth 1.1.

Note. It is not certain that the male belongs with the female.

Variation. The females from São Paulo have the sternum orange with a black patch, the sides of the abdomen black; the venter is light but with black spinnerets. Females vary in total length from 2.7 to 3.3 mm.

Diagnosis. The female is distinguished from *A. pedro* by the more rounded tip on the lobe of the epigynum (Fig. 234) and from *A. orgaos* by the flatter posterior plate (Fig. 235). The male is distinguished from *A. pedro* by the slightly curved rectangular median apophysis of the palpus and the round punctate terminal apophysis (Fig. 238).

Records. BRAZIL *São Paulo*: Jundiaí, Oct. 1976, 3♂ (A. Schneble, MCZ). *Rio Grande do Sul*: Farroupilha, 29 Sept. 1978, ♂ (W. Bischoff, MCN 8316).

Alpaida orgaos new species
Figures 239–242; Map 3

Holotype. Female from Serra dos Orgãos, 1,850 m, Est. Rio de Janeiro, Brazil, 19 April 1965 (H. Levi, ex MCZ, MZSP). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, legs orange. Dorsum of abdomen with median white band, sides white, and paired black patches (Fig. 241); venter with median black band enclosing spinnerets. Anterior median eyes 1.3 diameters apart; posterior median eyes their diameter apart. Abdomen oval, pointed behind (Fig. 241). Total length 5.7 mm. Carapace 2.3 mm long, 1.8 wide. First femur 1.7 mm; patella and tibia 2.3; metatarsus 1.4; tarsus 0.7. Second patella and tibia 2.0 mm; third 1.2; fourth 1.9.

Diagnosis. The female is distinguished

from *A. bischoffi* and others by the long scape (Fig. 239), and the sculpturing and shape of the posterior median plate of the epigynum (Fig. 240).

Alpaida sumare new species
Figures 243–245; Map 3

Holotype. Female from Sumaré, 200–300 m, Cidade Rio de Janeiro, Brazil, Feb. 1946 (H. Sick, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace light orange with paired brown marks. Chelicerae brown; labium, endites dark brown. Sternum brownish black. Coxae orange; legs light orange, distal part of femora brown, brown patches on underside of distal articles. Dorsum of abdomen white with symmetical black patches (Fig. 245); venter black. Posterior median eyes 1.5 diameters of others, which are subequal. Anterior median eyes their diameter apart; posterior median eyes 0.8 their diameter apart. Abdomen with shoulder humps and pointed posteriorly (Fig. 245). Total length 4.0 mm. Carapace 1.8 mm long, 1.3 wide. First femur 1.5 mm; patella and tibia 1.7; metatarsus 0.9; tarsus 0.5. Second patella and tibia 1.5 mm; third 1.1; fourth 1.5.

Diagnosis. Females are distinguished from *A. pedro* by a dark patch on each side of the head (Fig. 245), a more rounded median lobe of the epigynum, and the presence of an anterior margin on the lips on each side (Fig. 243).

Alpaida pedro new species
Figures 246–252; Map 3

Holotype. Female from Cerro Claro, São Pedro do Sul, Rio Grande do Sul, Brazil, 11 Jan. 1985 (A. A. Lise, MCN no. 12917). The specific name is a noun in apposition after the locality.

Description. Female. Carapace light orange with black mark between lateral and anterior median eyes. Sternum orange. Legs dusky orange-yellow, first two pairs darkest with venter black. Dorsum of abdomen contrasting black and white pigment (Fig. 249); sides black; venter with rectangular black mark framed by white; spinnerets black (Fig. 250). Anterior median eyes slightly more than their diameter apart; posterior median eyes their diameter apart. Abdomen with shoulder humps and posteriorly pointed (Fig. 249). Total length 4.0 mm. Carapace 1.6 mm long, 1.2 wide. First femur 1.3 mm; patella and tibia 1.7; metatarsus 1.0; tarsus 0.5. Second patella and tibia 1.5 mm; third 0.9; fourth 1.5.

Male. Carapace, sternum, legs orange-yellow. Legs indistinctly ringed. Dorsum of abdomen with black marks, no white pigment (Fig. 251); venter yellowish, spinnerets black. Posterior median eyes 0.8 diameter; lateral eyes 0.6 diameter of anterior medians. Anterior median eyes 0.6 diameter apart; posterior median eyes their diameter apart. Second tibiae not thicker than first. Total length 3.8 mm. Carapace 1.6 mm long, 0.8 wide. First femur 1.5 mm; patella and tibia 1.9; metatarsus 1.1; tarsus 0.5. Second patella and tibia 1.5 mm; third 1.0; fourth 1.6.

Note. The association of this male with the females of *A. pedro* is uncertain; they have not been collected together. All females are variable in color and epigynum shape and so are the four males. There may be several species.

Variation. Females vary from 3.0 to 3.8 mm, males from 3.5 to 3.8. Color pattern and shape of the epigynum vary considerably (Figs. 246, 248). Some specimens lack the black eye patches or the median ventral patch. Some males have white pigment on the abdomen.

Diagnosis. Females differ from *A. bischoffi* by notched and sharply pointed triangular lobe of the epigynum (Figs. 246, 248) and by the dark semicircle on each side dorsally on the posterior plate (Fig. 247). Males are distinguished by the shape of the long median apophysis, a lateral tip on the edge of the tegulum and a small rectangular terminal apophysis (Fig. 252).

Records. BRAZIL *Rio Grande do Sul*: Estação Exp. Fitotécnica de Águas Belas, Viamão, 13 Sept. 1984, ♀, 3 imm. (A. A. Lise, MCN); Morro do Coco, Viamão, 5

May 1978, ♀ (A. A. Lise, MCN 8236); São Francisco de Paula, 23 Jan. 1981, ♀ (A. A. Lise, MCN 9538); Carazinho, 10 Nov. 1979, ♀ (H. Bischoff, MCN); Parque Estadual de Nonoai, Nonoai, 14 Jan. 1985, ♀ (A. A. Lise, MCN 12819); Farroupilha, 29 Oct. 1978, ♀, ♂ (H. Bischoff, MCN 8317, 8319); Itaimbézinho, Cambará do Sul, 6 Jan. 1985, ♀ (A. A. Lise, MCN 12767); Vila Oliva, Caxias do Sul, 5 Jan. 1976, ♀ (P. A. Buckup, MCN 3696); Vacaria, 23 Oct. 1981, ♂ (A. A. Lise, MCN 11437); Porto Alegre, 13 Sept. 1975, ♂ (A. A. Lise, MCN 03014); Canela, 24 Aug. 1975, ♂ (A. A. Lise, MCN 3017).

Alpaida moka new species
Figures 253–256; Map 3

Holotype. Female from Nueva Moka, 350 m, Dpto. Santa Cruz, Bolivia [17°19'S, 63°33'W], Feb. 1951 (Prosen, MLP). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, legs yellow. Labium, sternum, endites black. Coxae light yellow. Dorsum of abdomen white with four dusky semi-circles on each side, posterior tip black (Fig. 255); venter with black band between epigynum and enclosing spinnerets (Fig. 256). Abdomen with posterior rounded tail (Fig. 255). Total length 4.5 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.7 mm; patella and tibia 1.9; metatarsus 1.3; tarsus 0.5. Second patella and tibia 1.5 mm; third 0.9; fourth 1.4.

Note. The only specimen has the epigynum standing up and its ventral surface facing anteriorly.

Diagnosis. The tiny lobe of the epigynum (Fig. 253) and the subtriangular posterior median plate (Fig. 254) separate this species from similar ones.

Alpaida haligera (Archer)
Figures 257–260; Map 3

Lariniacantha haligera Archer, 1971: 159, fig. 5, ♀. Female holotype from San Esteban, [Est. Carabobo] Venezuela (AMNH), examined.
Alpaida haligera:—Brignoli, 1983: 256.

Description. Female. Carapace orange-yellow. Sternum orange-yellow with a median black patch. First and second patella, tibia, metatarsi and tarsi black dorsally, otherwise yellow-orange with black spots. Dorsum of abdomen orange-yellow with black patches and some white pigment spots (Fig. 259); sides with black patches (Fig. 260); venter with gray marks in center. Anterior median eyes their diameter apart; posterior median eyes slightly more than their diameter apart. Abdomen with two anterior humps and a median posterior hump (Fig. 259). Total length 5.0 mm. Carapace 2.1 mm long, 1.7 wide. First femur 2.3 mm; patella and tibia 2.6; metatarsus 1.7; tarsus 0.7. Second patella and tibia 2.1 mm; third 1.4; fourth 2.2.

Diagnosis. This female is distinguished from others by the large pointed triangular lobe (Fig. 257) and by the rectangular posterior plate of the epigynum (Fig. 258).

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Figures 253–256. *Alpaida moka* n. sp., female. 253, epigynum, ventral. 254, epigynum, posterior. 255, dorsal.

Figures 257–260. *A. haligera* (Archer), female. 257, epigynum, ventral. 258, epigynum, posterior. 259, dorsal. 260, abdomen, lateral.

Figures 261-266. *A. banos* n. sp. 261–264, female. 261, epigynum, ventral. 262, epigynum, posterior. 263, dorsal. 264, ventral. 265, 266, male. 265, dorsal. 266, left palpus.

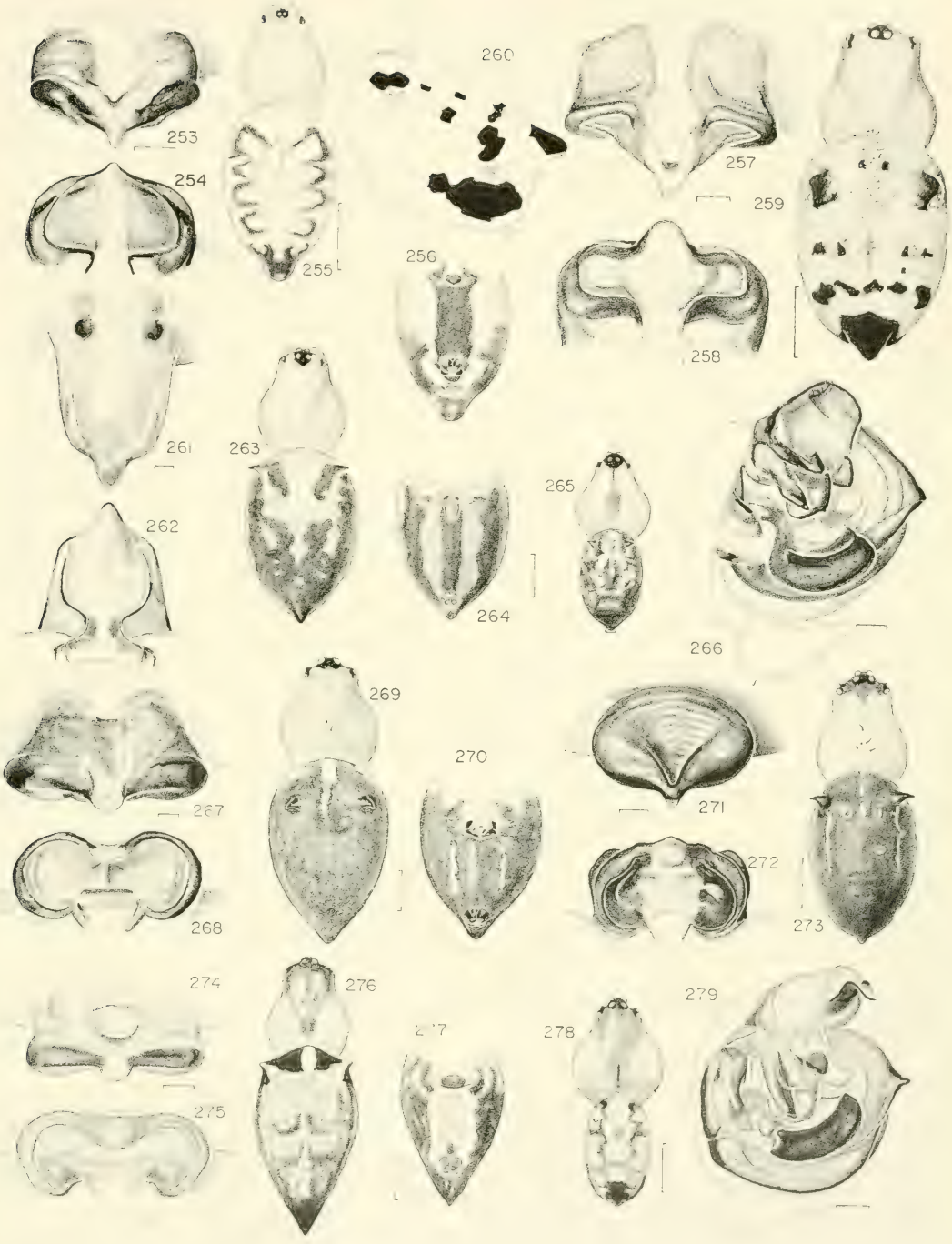
Figures 267–270. *A. cuyabeno* n. sp., female. 267, epigynum, ventral. 268, epigynum, dorsal. 269, dorsal. 270, ventral.

Figures 271–273. *A. narino* n. sp., female. 271, epigynum, ventral. 272, epigynum, posterior. 273, dorsal.

Figures 274–277. *A. amambay* n. sp., female. 274, epigynum, ventral. 275, epigynum, posterior. 276, dorsal. 277, ventral.

Figures 278–279. *A. gurupi* n. sp., male. 278, dorsal. 279, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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Alpaida banos new species
Figures 261–266; Map 4

Holotype. Female from Baños, Runtun, 2,300 m, 1°26'S, 78°24'W, Prov. Tungurahua, Ecuador, Dec. 1938 (W. Clarke-Macintyre, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum orange. Coxae dusky; legs dusky orange. Dorsum of abdomen orange and black with some white spots (Fig. 263); venter black in center with an orange band on each side, sides black (Fig. 264). Posterior median eyes 1.3 diameters of anterior medians; anterior laterals 0.8 diameter, posterior laterals 0.9 diameter of anterior medians. Anterior median eyes slightly less than their diameter apart; posterior medians their diameter apart. Abdomen with a pair of thorns on shoulders, pointed posteriorly (Fig. 263). Total length 6.4 mm. Carapace 2.5 mm long, 2.0 wide. First femur 2.2 mm; patella and tibia 2.9; metatarsus 1.9; tarsus 1.0. Second patella and tibia 2.5; third 1.7; fourth 2.9.

Male. Coloration as in female except dusky patch on thorax (Fig. 265). Posterior median eyes 0.8 diameter of anterior median eyes; anterior laterals 0.6, posterior laterals 0.5 diameter of anterior medians. Anterior median eyes slightly less than their diameter apart; posterior median eyes their diameter apart. Second tibiae slightly thicker than first, with macrosetae. Abdomen oval with a pair of spines on shoulders. Total length 4.2 mm. Carapace 2.1 mm long, 1.7 wide. First femur 2.0 mm; patella and tibia 2.5; metatarsus 1.5; tarsus 0.9. Second patella and tibia 1.9 mm; third 1.5; fourth 2.3.

Diagnosis. Males and females can be separated from most species by the anterior lateral thorns on the abdomen (Figs. 263, 265). The female is distinguished from those of *A. narino* by the longer than wide epigynum (Figs. 261, 262). The male palpus has gently curved median apophysis and the tegulum is pointed on the side (Fig. 266).

Paratype. ECUADOR *Los Ríos*: Playas de Juan, Montalvo, 15 m, March 1938, ♂ (W. Clarke-Macintyre, AMNH).

Alpaida cuyabeno new species
Figures 267–270; Map 4

Holotype. Female from Reserva Forestal Cuyabeno, Laguna Grande, Napo, Ecuador, 13 Feb. 1984 (L. Avilés, MECN). The specific name is a noun in apposition after the locality.

Description. Carapace, sternum orange. Chelicerae distally black. Coxae black, fourth one orange; legs black. Dorsum of abdomen black with three white marks anterior, two on sides (Fig. 269); sides black; venter black with two colorless light lines (Fig. 270). Posterior median eye area projecting; some setae in center of thorax. Posterior median eyes 1.2, anterior lateral eyes 0.7, posterior lateral eyes 0.8 diameter of anterior median eyes. Fourth legs longer than first. Abdomen with two pointed tubercles on shoulders and posterior hump (Fig. 269). Total length 7.6 mm. Carapace 3.1 mm long, 2.3 wide. First femur 2.7 mm; patella and tibia 3.4; metatarsus 2.3; tarsus 1.2. Second patella and tibia 2.9 mm; third 2.1; fourth 3.6.

Diagnosis. Unlike most species, *A. cuyabeno* has a thorn on each shoulder of the abdomen (Fig. 269); it differs from *A. banos* and *A. narino* by the shape of the epigynum; the lips are in an almost straight transverse line (Fig. 267) while those of *A. narino* are V-shaped.

Alpaida narino new species
Figures 271–273; Map 4

Holotype. Female from near Barbacoas, 20 m, Dpto. Nariño, Colombia, 20 March, 1974 (W. Eberhard no. 737, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellow, eye region black; chelicerae proximal half yellow, distal black; labium, endites, coxae, legs black. Sternum black, posteriorly yellow. Dorsum of abdomen black, a median anterior longitudinal white line and paraxial lateral pair of pigmentless lines (Fig. 273); sides with an anterior white

line; venter black. Carapace with several macrosetae on middle of thorax. Lateral eyes, 0.7 diameter; posterior median eyes 1.5 diameters of anterior median eyes. Anterior median eyes less than one diameter apart; posterior median eyes more than one diameter apart. Abdomen with pair of anterior recurved thorns and posterior median hump (Fig. 273). Total length 5.4 mm. Carapace 2.5 mm long, 1.7 wide. First femur 2.1 mm; patella and tibia 2.4; metatarsus 1.7; tarsus 0.9. Second patella and tibia 2.1 mm; third 1.5; fourth 2.5.

Diagnosis. Females differ from *A. banos* by having an oval epigynum with a V-shaped ventral notch (Fig. 271).

Alpaida amambay new species
Figures 274–277; Map 3

Holotype. Female from 10 km south of Bella Vista, Dpto. Amambay, Paraguay, 11 Oct. 1979 (Exped. Mus. Genève, MNHG). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellowish with dusky to black marks. Endites black; sternum yellow with white pigment. Coxae yellowish with dusky patches, second black; leg ringed black and yellowish. Dorsum of abdomen with white cardiac mark between black, behind this gray grading into black posteriorly (Fig. 276). Sides black; venter with two white lines, one on each side of pigmentless area (Fig. 277). Posterior median eyes 1.5 diameters of others, which are subequal. Fourth leg longer than first. Abdomen shield-shaped, pointed behind, with pointed shoulder humps and hump dorsally in front of posterior tip (Fig. 276). Total length 6.3 mm. Carapace 2.7 mm long, 2.0 wide. First femur 2.0 mm; patella and tibia 2.5; metatarsus 1.7; tarsus 0.9. Second patella and tibia 2.3 mm; third 1.8; fourth 2.9.

Diagnosis. Females have a narrower abdomen (Fig. 276) than the related species *A. cuyabeno* and *A. narino* and the notch of the epigynum is anterior to the nearly straight posterior edge (Fig. 274).

Alpaida gurupi new species
Figures 278, 279; Map 3

Holotype. Male from Canindé, Rio Gurupi, Pará, Brazil, 27–28 Feb. 1966 (B. Malkin, AMNH). The specific name is a noun in apposition after the locality.

Description. Male. Carapace orange with head and middle of thorax dusky. Sternum orange, with median black streak. Coxae, legs dusky orange. Dorsum of abdomen with pattern of black lines and white pigment spots (Fig. 278); venter with square black area bordered on each side by longitudinal orange band, black on each side. Anterior median eyes 0.8 their diameter apart; posterior median eyes their diameter apart. Second tibiae thicker than first, with macrosetae. Abdomen oval. Total length 4.0 mm. Carapace 2.1 mm long, 1.6 wide. First femur 2.0 mm; patella and tibia 2.5; metatarsus 1.5; tarsus 0.8. Second patella and tibia 1.8 mm; third 1.6; fourth 2.4.

Diagnosis. This male is distinguished from other species of *Alpaida* by the gently curved median apophysis and the hooded appearance of the terminal apophysis (Fig. 279).

Alpaida marmorata (Taczanowski), new combination
Figures 280–288; Map 4

Singa marmorata Taczanowski, 1873, 125, ♀. Female holotype from Uassa, French Guiana [Uaça, Amapá, Brazil] (PAN), examined. Roewer, 1942: 877.
Araneus marmoratus:—Bonnet, 1955: 534.

Note. The vial of the holotype was labeled "?*Singa* juvenile" without a specific name. However, the contents of the vial fit the description of the species. The vial has been relabeled.

Description. Female. Carapace yellow, with reticulated pattern, brown on each side of head. Sternum blackish-brown. Legs with fine dark rings, broken on dorsum. Dorsum of abdomen white with two jagged black lines (Fig. 286); venter black with a white patch on each side of pedicel.

Anterior median eyes 0.7 diameter apart, posterior medians their diameter apart. Abdomen longer than wide with a pair of low shoulder humps and a posterior median hump (Fig. 287). Total length 5 mm. Carapace 1.6 mm long, 1.4 wide. First femur 1.8 mm; patella and tibia 2.0; metatarsus 1.2; tarsus 0.6. Second patella and tibia 1.8 mm; third 1.2; fourth 1.9.

Variation. All three specimens are between 4.9 and 5.0 mm total length. The shape of the lip is variable (Figs. 280–285). One specimen lacks shoulder humps.

Diagnosis. The epigynum has the lip turned up (Fig. 285), unlike that of any other species. Perhaps a median lobe was torn off.

Records. ECUADOR *Napo*: Río Tarapuy, Feb. 1983, ♀ (L. Avilés, MECN). PERU *Huánuco*: Tingo María, 10 Jan. 1947, ♀ (J. C. Pallister, AMNH).

Alpaida simla new species
Figures 289–293; Map 4

Holotype. One female holotype, one male, six immature paratypes from Simla, Trinidad, Lesser Antilles, April 1964 (A. M. Chickering, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange, head and rim of thorax black. Sternum orange, sides dusky; endites black. Coxae dusky on orange; legs orange with femora and patellae dusky. Dorsum of abdomen with black pattern and pairs of white spots (Fig. 291); venter, black. Anterior lateral eyes and posterior lateral eyes 0.8; posterior median eyes 1.5 diameters of anterior median eyes. Fourth legs longer than first. Abdomen oval, pointed behind overhanging spinnerets (Fig. 291). Total length 4.8 mm. Carapace 2.2 mm long, 1.5 wide. First femur 2.0 mm; patella and tibia 2.3; metatarsus 1.6; tarsus 0.9. Second patella and tibia 2.1 mm; third 1.6; fourth 2.5.

Male. Coloration as in female (Fig. 292). Venter with a pair of pigmentless lines, one on each side. First and second tibiae thick with some macrosetae. Total length 4.2 mm. Carapace 2.1 mm long, 1.7 wide. First femur 2.3 mm; patella and tibia 2.3; metatarsus 1.6; tarsus 0.9. Second patella and tibia 1.9 mm; third 1.7; fourth 2.5.

Variation. Total length of females from 4.7 to 4.8 mm, males 4.1 to 4.2.

Diagnosis. The species differs from similar species by having the sides of the thorax black (Figs. 291, 292). Females differ by the large median lobe of the epigynum, larger than the lateral lobes (Fig. 289). Males differ by the curved median apophysis, with two sides parallel, and by the wide embolus (Fig. 293).

Natural History. A male was collected with a pit-fall trap.

Paratypes. LESSER ANTILLES *Trinidad*: Port of Spain, 1913, ♀ (R. Thaxter, MCZ); Spring Hill, Arima, 18–19 July 1979, ♂ (L. N. Sorkin, AMNH).

Alpaida hartliebi new species
Figures 294–297; Map 4

Holotype. Female holotype and two female, two immature paratypes from Porto Alegre, Rio Grande

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Figures 280–288. *Alpaida marmorata* (Taczanowski), female. 280–282, epigynum, ventral. 283, 284, epigynum, posterior. 285, epigynum, lateral. 286, 287, dorsal. 288, ventral. 280, 283, 285, 286 (syntype). 281, 284, 287, 288, (Peru). 282, (Ecuador).

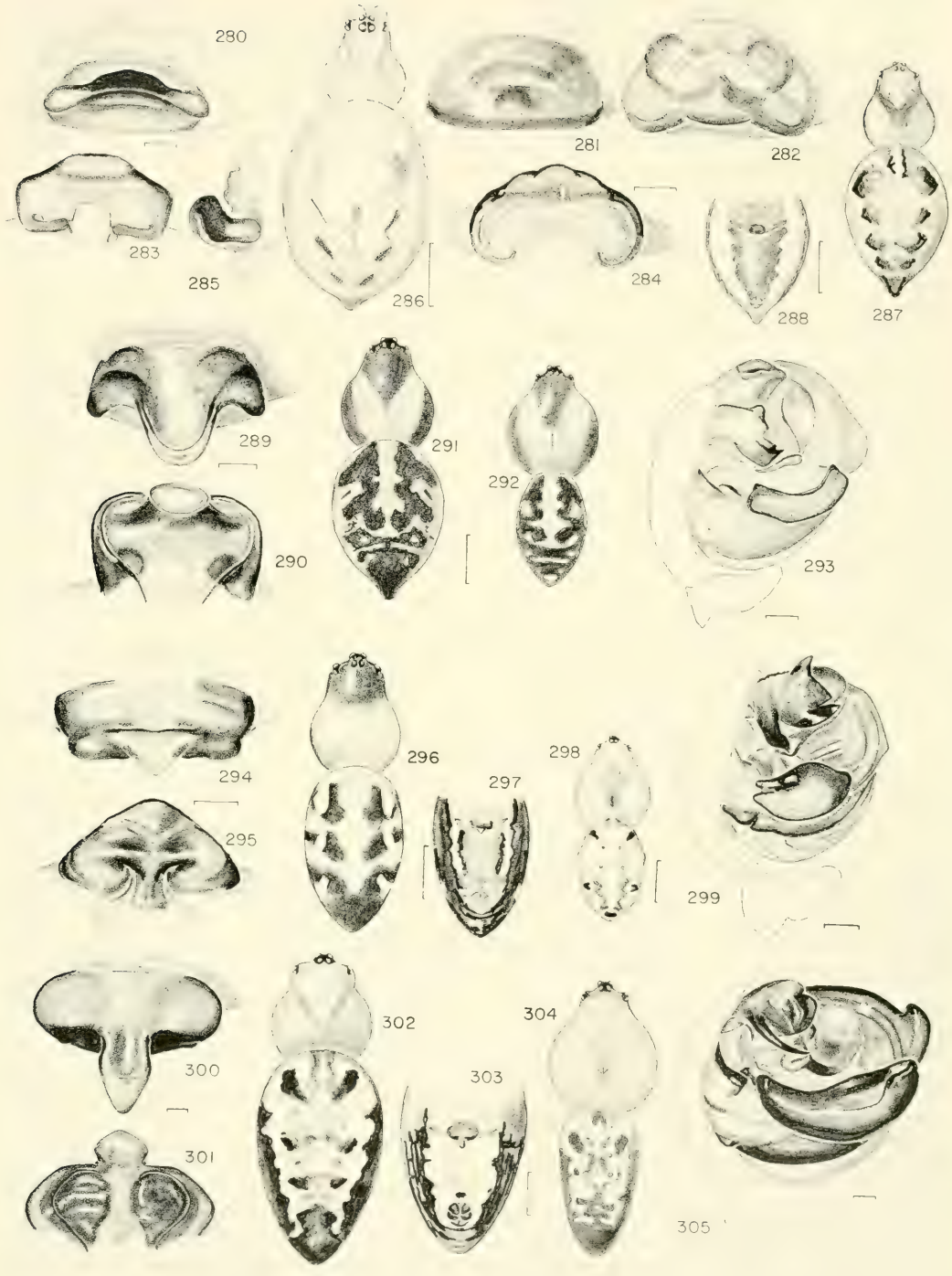
Figures 289–293. *A. simla* n. sp. 289–291, female. 289, epigynum, ventral. 290, epigynum, posterior. 291, dorsal. 292, 293, male. 292, dorsal. 293, left palpus.

Figures 294–297, *A. hartliebi* n. sp. 294–297, female. 294, epigynum, ventral. 295, epigynum, posterior. 296, dorsal. 297, ventral.

Figures 298, 299. *A. jacaranda* n. sp., male. 298, dorsal. 299, palpus.

Figures 300–305. *A. gallardoi* n. sp. 300–303, female. 300, epigynum, ventral. 301, epigynum, posterior. 302, dorsal. 303, ventral. 304, 305, male. 304, dorsal. 305, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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do Sul, Brazil, 16 Nov. 1963 (C. A. Hartlieb, MCN no. 1282). The species is named after the collector.

Description. Female. Carapace orange with black head and rim. Chelicerae, labium, endites black. Sternum, legs dusky orange; coxae darker dusky orange. Dorsum of abdomen with pairs of black and pairs of white patches (Fig. 296), venter with two parallel white bands (Fig. 297). Carapace narrower in eye region than other species. Anterior median eyes and posterior median eyes each 1.5 diameters apart. Fourth legs slightly longer than first. Abdomen pointed behind (Fig. 296). Total length 5.2 mm. Carapace 2.0 mm long, 1.5 wide. First femur 1.8 mm; patella and tibia 2.1; metatarsus 1.4; tarsus 0.8. Second patella and tibia 1.9 mm; third 1.3; fourth 2.2.

Note. The type specimens are in poor physical condition. The tip of the epigynum appears loosely attached and probably tears off.

Diagnosis. Females distinguished from those of the similar *A. gallardoi* by the straight transverse lip of the epigynum (Fig. 294) and the transverse swelling of the posterior plate (Fig. 295).

Alpaida jacaranda new species
Figures 298, 299; Map 4

Holotype. Male from Fazenda Jacaranda, Itamarajú, Bahia, Brazil, 9 Dec. 1977 (J. S. Santos, MCN no. 11032). The specific name is a noun in apposition after the locality.

Description. Male. Carapace orange with darker patch in middle. Sternum orange with white pigment. Legs orange. Dorsum of abdomen with white pigment on gray, five dusky spots and a pair of dusky zig-zag lines (Fig. 298); venter black with white spot on each side of spinnerets. Anterior median eyes and posterior lateral eyes subequal; anterior laterals 0.8 diameter; posterior median eyes 1.3 diameters of anterior medians. Anterior median eyes 0.6 their diameter apart; posterior median eyes 0.8 their diameter apart. Legs thick; venter of second femora with short macrosetae, 5 on one side, 14 on other; second tibiae with macrosetae; fourth trochanters with two short macrosetae. Abdomen oval, pointed behind (Fig. 298). Total length 4.5 mm; carapace 2.2 mm long, 1.7 wide. First femur 2.2 mm; patella and tibia 2.5; metatarsus 1.5; tarsus 0.7. Second patella and tibia 2.0 mm; third 1.3.

Diagnosis. The ovoid median apophysis, slightly pointed on each end, with a small finger projecting toward the cymbium (Fig. 299), is distinctive.

Alpaida gallardoi new species
Figures 300–305; Map 4

Holotype. Female holotype and two female paratypes from Bella Vista, Prov. Buenos Aires, Argentina, Jan. 1966 (J. M. Gallardo, MACN nos. 8490, 8491). The species is named after the collector.

Description. Female. Carapace, sternum orange. Coxae orange with black spots; legs with contrasting black and orange rings. Dorsum of abdomen with paired black spots (Fig. 302); sides black, anterior orange, sides orange-white; venter orange-white, black on sides. Posterior median eyes 1.5 diameters of anterior median eyes. Abdomen oval, posteriorly pointed (Fig. 302). Total length 7.0 mm. Carapace, 2.8 mm long, 2.2 wide. First femur 2.4 mm; patella and tibia 2.7; metatarsus 1.8; tarsus 0.9. Second patella and tibia 2.5 mm; third 1.8; fourth 2.8.

Male from Rio Grande do Sul. Coloration as in female (Fig. 304). Total length 6.5 mm. Carapace 3.2 mm long, 2.5 wide. First femur 2.9 mm; patella and tibia 3.6. Second patella and tibia 2.7 mm; third 2.0; fourth 3.3.

Variation. Total length of females varies from 5.6 to 8.0 mm, of males from 6.3 to 6.5. Some specimens have a black mark in the center of the light venter of the abdomen.

The holotype female and a male from Rio Grande do Sul (MCN) are described and illustrated.

Diagnosis. Females differ from those of *A. hartliebi* and others by the parallel margin of the scape and the dark lip on each side in ventral view (Fig. 300). Males differ

by a very large boat-shaped median apophysis (Fig. 305), a lobe on the margin of the tegulum and a small round terminal apophysis (Fig. 305).

Natural History. Specimens have been collected in Paraguay in undisturbed tall forest.

Paratypes. BRAZIL *Santa Catarina*: Pinhal, Dec., Jan. 1947–1949, 6♀ (A. Maller, AMNH, MCZ). *Rio Grande do Sul*: Garruchos, São Borja, 10 Dec. 1975, 5♀, ♂ (A. A. Lise, MCN); Montenegro, 3 Nov. 1977, ♀ (H. A. Gastral, MCN); Santo Leopoldo, Nov., Dec. 1964, 3♀ ♂ (C. Volla, MZSP). PARAGUAY *Paraguarí*: Parque Nac. Ybyauí, 28 Sept. 1985, ♀ (J. A. Kochalka, MNHNP). ARGENTINA *Buenos Aires*: La Plata, ♀ (Blanco, MLP); Ranelagh, 3 Mar. 1963, ♀ (O. de Ferrariis, AMNH).

Alpaida sobradinho new species
Figures 306–309; Map 4

Holotype. Female from Sobradinho, Rio Grande do Sul, Brazil, 10 Jan. 1985 (A. A. Lise, MCN no. 12886). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange-yellow; sides of head and groove between head and carapace dusky. Labium, chelicerae, endites dusky. Sternum orange with dusky sides. Coxae orange-yellow; legs orange-yellow with black rings. Dorsum of abdomen black with orange shoulder patches and an orange mark on each side behind shoulder patch (Fig. 308); sides black; venter orange-yellow between genital groove and spinnerets, underlain by white pigment spots (Fig. 309). Abdomen oval, pointed behind. Total length 6.0 mm. Carapace 2.3 mm long, 1.8 wide. First femur 1.9 mm; patella and tibia 2.3; metatarsus 1.3; tarsus 0.8. Second patella and tibia 1.9 mm; third 1.3; fourth 2.0.

Diagnosis. This female is distinguished from those of *A. gallardoi* and *A. hartliebi* by the small lobe on the epigynum (Fig. 306) and the two circular bulges that form the posterior plate (Fig. 307).

Alpaida itapua new species
Figures 310–312; Map 4

Holotype. Female from km A436, Centro Forestal, Pirapó, Dpto. Itapúa, Paraguay, 4 Aug. 1982 (J. A. Kochalka, MNHNP). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, coxae orange. Legs with black and yellowish white rings of equal width. Dorsum of abdomen with six black patches surrounded by indistinct black spots on white, and a posterior black tip (Fig. 312). Venter black with a colorless longitudinal line on each side. Eyes subequal in size. Anterior median eyes their diameter apart; posterior median eyes their diameter apart. Abdomen oval, pointed behind. Total length 8.0 mm. Carapace 3.6 mm long, 3.1 wide. First femur 2.7 mm; patella and tibia 3.4; metatarsus 1.9; and tarsus 0.9. Second patella and tibia 3.0 mm; third 2.1; fourth 3.1.

Diagnosis. Females differ from *A. alto* by the small set-off median lobe and transverse, almost straight, posterior edge (Fig. 310).

Natural History. Kochalka (in letter) found the specimen in undisturbed forest among the roots and bases of trees. The small webs are a few inches above the ground and have a line going from the hub to a retreat that is located in a convenient cavity in the substrate. The spider is at the hub day and night and runs to the retreat when disturbed. It had a red cephalothorax, and black and yellow legs when alive. Owners of other webs were not collected.

Alpaida picchu new species
Figures 313–316; Map 4

Holotype. Female from Torontoy Canyon, base of Machu Picchu, 2,000 to 2,200 m, Depto. Cuzco, Peru, 19–23 June 1964 (B. Malkin, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, coxae orange. Legs dusky orange-brown. Dorsum of abdomen maculated black with three white marks anteriorly

(Fig. 315); venter with white pigment enclosing three black patches (Fig. 316), sides black. Posterior median eyes 1.3 diameters of anterior median eyes; lateral eyes 0.8 diameter of anterior medians. Anterior median eyes their diameter apart; posterior median eyes slightly more than their diameter apart. Abdomen [damaged] oval, pointed behind, with shoulder humps (Fig. 315). Total length 6.0 mm. Carapace 2.6 mm long, 2.0 wide. First femur 2.1 mm; patella and tibia 2.7; metatarsus 1.5; tarsus 0.9. Second patella and tibia 2.1; third 1.8; fourth 2.6.

Diagnosis. *Alpaida picchu* differs from *A. alto* and *A. itapua* by having the two margins of the lips of the epigynum parallel in ventral view (Fig. 313) and having a median groove on the bulging lips, with the lobe depressed, visible in posterior view (Fig. 314).

Alpaida sevilla new species
Figures 317–319; Map 4

Holotype. Female from Sevilla, Dpto. Valle, Colombia, 25 July 1926 (E. W. Walker, AMNH). The specific name is a noun in apposition after the locality.

Description. Female. Carapace blackish brown with sides of thorax lighter brown. Labium, sternum, endites dark brown. Coxae yellow; legs yellow-brown ringed with black. Dorsum of abdomen white with black marks (Fig. 319); venter black with white marks on sides of spinnerets and white behind spinnerets. Posterior median eyes 1.2 diameters; lateral eyes 0.9 diameter of anterior medians. Anterior median eyes slightly more than their diameter apart; posterior median eyes slightly less than their diameter apart. Abdomen with shoulder humps and pointed behind (Fig. 319). Total length 4.6 mm. Carapace 1.9 mm long, 1.5 wide. First femur 1.4 mm; patella and tibia 1.9; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.6 mm; third 1.1; fourth 1.7.

Diagnosis. Females are distinguished from similar species by the tripartite posterior median plate of the epigynum (Fig. 318).

Alpaida alto new species
Figures 320–323; Map 4

Holotype. Female from km 12, de Stroessner, Centro Forestal de Alto Paraná, Dept. Alto Paraná, Paraguay, 22 July 1982 (J. A. Kochalka, MNHNP). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange with a black pattern on head; labium black; sternum orange. Endites, coxae black; legs ringed with black and light orange. Dorsum of abdomen with black patches and streaks, cardiac area white (Fig. 322); venter black with a pair of parallel white lines (Fig. 323). Secondary eyes are 0.8 diameters of anterior median eyes. Anterior median eyes slightly less than their diameter apart, posterior median eyes their diameter apart. Abdomen oval, pointed behind (Fig. 322). Total length 8.4 mm. Carapace 3.7 mm long, 2.8 wide. First femur 3.4 mm; patella and tibia 4.0; metatarsus 2.7; tarsus 1.2. Second patella and tibia 3.7 mm; third 2.5; fourth 3.9.

Diagnosis. Females are distinguished from similar species with similar coloration by the epigynum whose median lobe has margins which continue laterally into

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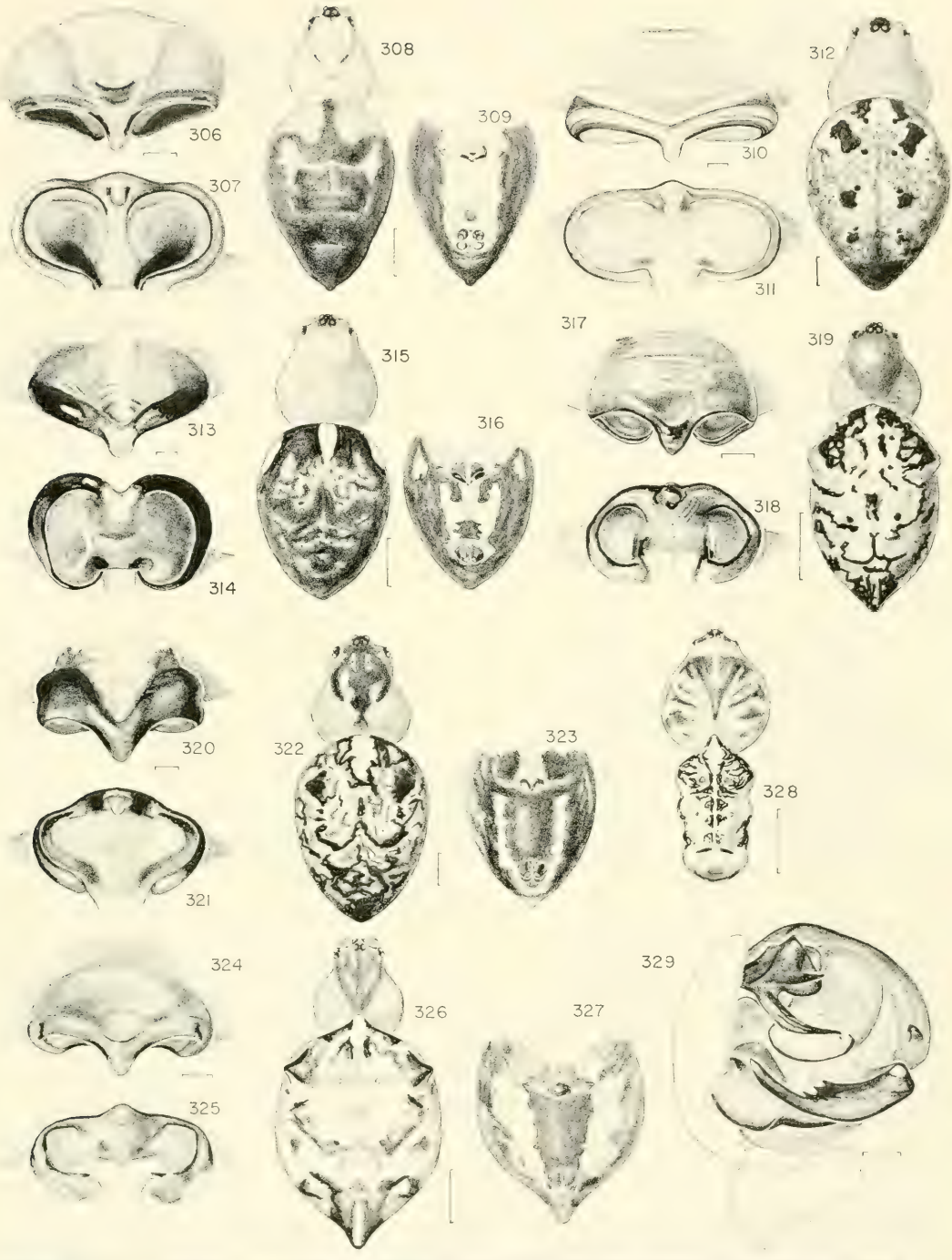
Figures 306–309. *Alpaida sobradinho* n. sp., female. 306, epigynum, ventral. 307, epigynum, posterior. 308, dorsal. 309, ventral.

Figures 310–312. *A. itapua* n. sp., female. 310, epigynum, ventral. 311, epigynum, posterior. 312, dorsal.

Figures 313–316. *A. picchu* n. sp., female. 313, epigynum, ventral. 314, epigynum, posterior. 315, dorsal. 316, ventral.

Figures 317–319. *A. sevilla* n. sp., female. 317, epigynum, ventral. 318, epigynum, posterior. 319, dorsal.

Figures 320–323. *A. alto* n. sp., female. 320, epigynum, ventral. 321, epigynum, posterior. 322, dorsal. 323, ventral.



Figures 324–327. *A. thaxteri* n. sp., female. 324, epigynum, ventral. 325, epigynum, posterior. 326, dorsal. 327, ventral.

Figures 328, 329. *A. boraceia* n. sp., male. 328, dorsal. 329, left palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

a concave posterior edge; the posterior tip of the notch is in line with the posterior edge and in posterior view the lips are slightly swollen dorsally (Fig. 321).

Alpaida thaxteri new species
Figures 324–327; Map 4

Holotype. Female holotype and one female paratype from Port of Spain, Trinidad, Lesser Antilles, 1913 (R. Thaxter, MCZ). The species is named after the collector.

Description. Female. Carapace yellow with black pattern on head. Chelicerae with anterior black patch and tip black. Labium, endites, sternum, black. Legs yellowish with narrow dusky rings. Dorsum of abdomen marked black and white (Fig. 326); venter black with white on sides (Fig. 327). Lateral eyes 0.8 diameter of median eyes. Abdomen with anterior pair of humps on anterior median and posterior median tubercle. Total length 6.0 mm. Carapace 2.2 mm long, 1.7 wide. First femur 1.9 mm; patella and tibia 2.3; metatarsus 1.5; tarsus 0.7. Second patella and tibia 1.9 mm; third 1.4; fourth 2.0.

Diagnosis. Unlike *A. wenzeli* the margin of the lips are parallel and the lips of the epigynum continue into the median lobe (Fig. 324).

Alpaida boraceia new species
Figures 328, 329; Map 4

Holotype. Male from Boraceia, Salesópolis, 800 m, Est. São Paulo, Brazil, 21–25 Oct. 1963 (M. Oliveira, P. Wygodzinsky, AMNH). The specific name is a noun in apposition after the locality.

Description. Male. Carapace orange with brown streaks, a light orange transverse band behind eyes (Fig. 328). First coxae dusky, others black; legs orange, indistinctly ringed dark brown, first and second tibiae black. Dorsum of abdomen with median white line, irregular black blotches to side of line (Fig. 328); venter orange. Second tibiae thicker than first with macrosetae. Abdomen anteriorly pointed, sides wavy (Fig. 328). Total length 3.8 mm. Carapace 2.1 mm long, 1.7 wide. First femur 2.3 mm; patella and tibia 2.8; metatarsus 1.6; tarsus 0.7. Second patella and tibia 2.1 mm; third 1.3; fourth 1.8.

Diagnosis. This male distinguished from others of the species group by the carapace markings (Fig. 328) and by the structure of the palpus, which has a long median apophysis with an extension toward the cymbium and a small angular terminal apophysis (Fig. 329).

Alpaida iguazu new species
Figures 330–335; Map 4

Holotype. Female holotype and one juvenile paratype from Puerto Iguazú, Prov. Misiones, Argentina, Oct. 1953 (Schiapelli, Galiano, MACN no. 3907). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange with black pattern (Fig. 332). Labium, endites black. Sternum orange with median black patch. Coxae orange with dark marks; legs with narrow orange and black rings. Dorsum of abdomen with white cardiac mark, mottled gray and black (Fig. 332); venter black with a pair of pigmentless bands approaching each other posteriorly (Fig. 333). Abdomen oval pointed behind, with slight shoulder humps (Fig. 332). Total length 5.8 mm. Carapace 2.6 mm long, 2.0 wide. First femur 2.1 mm; patella and tibia 2.7; metatarsus 1.6; tarsus 0.8. Second patella and tibia 2.3 mm; third 1.6; fourth 2.5.

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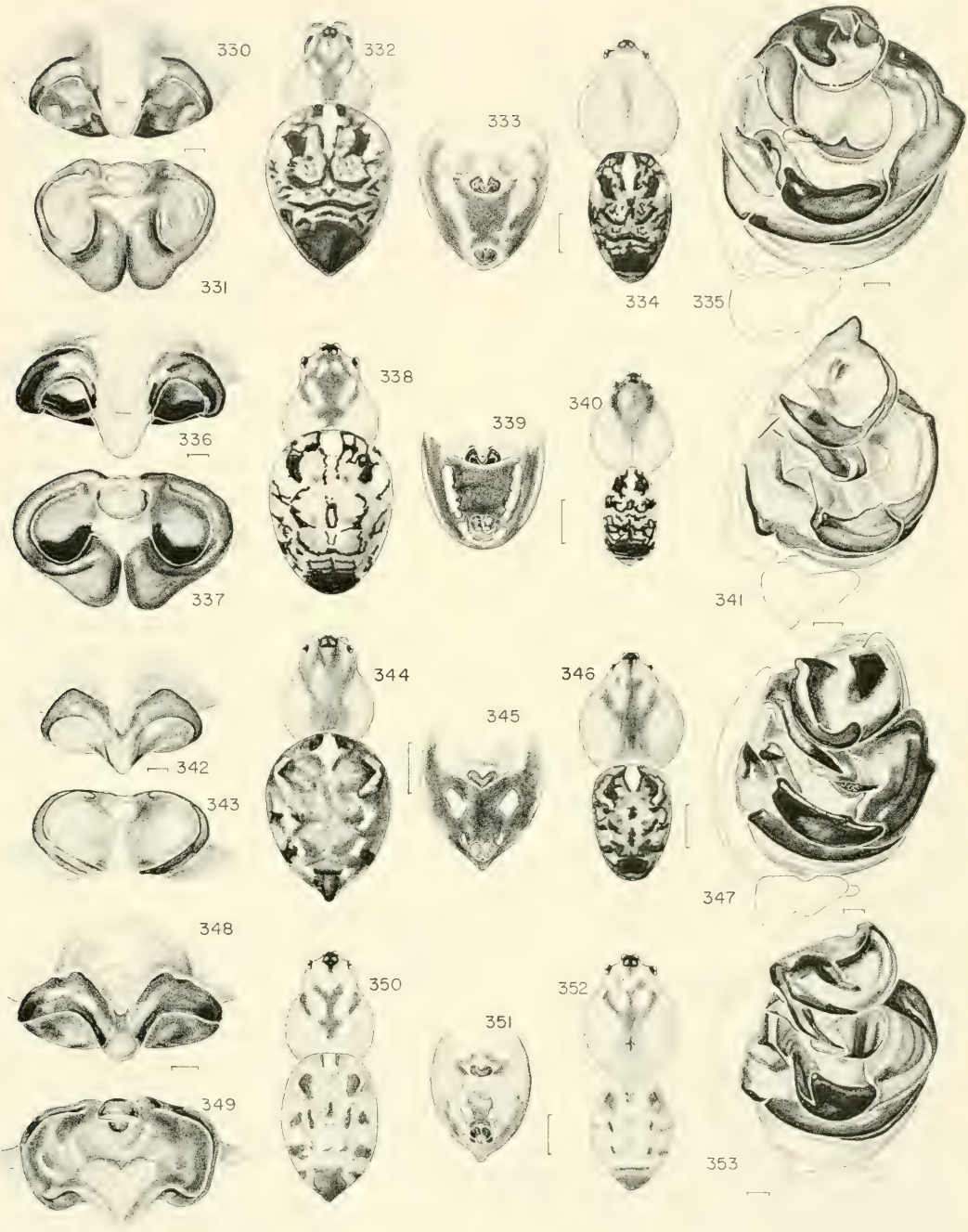
Figures 330–335. *Alpaida iguazu* n. sp. 330–333, female. 330, epigynum, ventral. 331, epigynum, posterior. 332, dorsal. 333, ventral. 334–335, male. 334, dorsal. 335, left palpus.

Figures 336–341. *A. tijuca* n. sp. 336–339, female. 336, epigynum, ventral. 337, epigynum, posterior. 338, dorsal. 339, ventral. 340, 341, male. 340, dorsal. 341, palpus.

Figures 342–345. *A. wenzeli* n. sp., female. 342, epigynum, ventral. 343, epigynum, posterior. 344, dorsal. 345, ventral.



Figures 346, 347. *A. caxias* n. sp., male. 346, dorsal. 347, palpus.

Figures 348–353. *A. canoa* n. sp. 348–351, female. 348, epigynum, ventral. 349, epigynum, posterior. 350, dorsal. 351, ventral. 352, 353, male. 352, dorsal. 353, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

Male. Coloration as in female but carapace with less black (Fig. 334). Total length 5.9 mm. Carapace, 3.1 mm long, 2.5 mm wide. First femur 3.0 mm; patella and tibia 3.6; metatarsus 2.1; tarsus 1.1. Second patella and tibia 2.9 mm; third 2.2; fourth 3.1.

Note. The male was not collected with the female but it has a similar color pattern. The female holotype and the male from Misiones Prov. are described and illustrated.

Variation. Total length of females from 5.8 to 7.0 mm. The largest are specimens from Petrópolis, which have a pattern as in this species. The venter of epigynum of these specimens is more like that of *A. rosa* and the posterior bulges are smaller.

Diagnosis. Unlike similar species, the median end of the rim of the epigynum is swollen in posterior view (Fig. 331). This swelling is longer and narrower (Fig. 331) than that of *A. tijuca*. The median apophysis of the palpus, unlike that of *A. caxias*, is from 5 to 7 o'clock in the circle of the palpus, and the basal curved prong (between 11 and 12 o'clock) of the terminal apophysis is shorter (Fig. 335).

Paratypes. BRAZIL *Rio de Janeiro*: Petrópolis, 2♀ (MNRJ). *Santa Catarina*: Pinhal, Jan. 1948, 2♀ (A. Maller, AMNH). *Rio Grande do Sul*: Itaúba, Arroio de Tigre, 11 Apr. 1978, ♀ (A. A. Lise, MCN 7947). ARGENTINA *Misiones*: [no locality] 1958, ♂ (R. V. Partridge, MACN 8487).

Alpaida tijuca new species
Figures 336–341; Map 4

Holotype. Female holotype and one male paratype from Tijuca, Est. Rio de Janeiro, Brazil (M. Eugenio, MNRJ no. 58146). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange with black markings (Fig. 338). Chelicerae orange-yellow with median black patch. Labium, endites black. Sternum orange with black border and black central spot. Coxae orange-yellow; legs ringed black and orange. Dorsum of abdomen with black pattern and white pigment spots (Fig. 338); venter black with two pigmentless lines approaching each other posteriorly. Anterior median eyes 0.8 their diameter apart; posterior median eyes 0.6 their diameter apart. Abdomen oval. Total length 5.9 mm. Carapace 2.7 mm long, 2.2 wide. First femur 2.5 mm; patella and tibia 2.9; metatarsus 1.9; tarsus 0.9. Second patella and tibia 2.5 mm; third 1.7; fourth 2.5.

Male. Coloration as in female (Fig. 340). Eye sizes as in female. Second tibiae with macrosetae. Fourth trochanters with a short macroseta. Total length 4.5 mm. Carapace 2.4 mm long, 1.8 wide. First femur 1.9 mm; patella and tibia 2.3; metatarsus 1.3; tarsus 0.7. Second patella and tibia 1.8 mm; third 1.5; fourth 2.1.

Variation. Females vary in total length from 5.9 to 7.4 mm. The females from Petrópolis have slight shoulder humps with the posterior hump more distinct.

The holotype and male paratype are illustrated and described.

Diagnosis. The female is distinguished from most *Alpaida* by the swollen median dorsal ends of the epigynum (Fig. 337), and from *A. iguazu* by the shorter and wider swellings. The male is distinguished by the dentate distal tooth of the terminal apophysis (Fig. 341).

Paratypes. BRAZIL *Rio de Janeiro*: Petrópolis, 2♀ (MNRJ 286); [?] Faxenda da Castaneira, ♀ (P. Peterson, ZMK).

Alpaida wenzeli (Simon), new combination
Figures 342–345; Map 4

Araneus wenzeli Simon, 1897a: 874. Nine female, 10 juvenile syntypes from St. Vincent Island, Lesser Antilles (BMNH), examined.
Aranea wenzeli:—Roewer, 1942: 856.

Description. Female. Head and thorax mostly black (Fig. 344), sides of thorax yellowish. Labium, sternum, endites black. Coxae yellowish. Legs ringed black and yellow. Dorsum of abdomen mostly dusky to black with a white cardiac mark and pairs of white spots, which approach each other posteriorly (Fig. 344). Venter black with a pair of white patches (Fig. 345).

Anterior median eyes their diameter apart; posterior median eyes slightly less than their diameter apart. Abdomen with shoulder humps and posterior tip. Total length 5.2 mm. Carapace 2.1 mm long, 1.8 wide. First femur 2.1 mm; patella and tibia 2.5; metatarsus 1.6; tarsus 0.8. Second patella and tibia 2.0 mm; third 1.3; fourth 2.2.

Diagnosis. The epigynum of *A. wenzeli* in ventral view is similar to that of *A. haligera*, but *A. wenzeli* has wider lips in ventral view (Fig. 342), narrower in posterior view (Fig. 343).

Alpaida caxias new species
Figures 346, 347; Map 4

Holotype. Male from Duque de Caxias, Est. Rio de Janeiro, Brazil, 5 Sept. 1961 (M. Alvarenga, AMNH). The specific name is a noun in apposition after the locality.

Description. Male. Carapace orange with dark brown pattern. Sternum orange with median black streak. Coxae orange, legs orange with dark brown rings. Dorsum of abdomen black mottled on gray with white cardiac mark (Fig. 346); venter black. Posterior median eyes 0.8; lateral eyes 0.6 diameter of anterior median eyes. Anterior median eyes slightly less than their diameter apart; posterior median eyes their diameter apart. Second tibiae slightly thicker than first with macrosetae. Total length 5.2 mm. Carapace 2.9 mm long, 2.3 wide. First femur 2.7 mm; patella and tibia 3.2; metatarsus 1.9; tarsus 0.9. Second patella and tibia 2.5 mm; third 1.9; fourth 2.7.

Diagnosis. This male differs from similar species by having the median apophysis shifted toward the cymbium from 5 to 7 o'clock on the circular palpus and having a heavy curved basal prong on the terminal apophysis (Fig. 347).

Alpaida canoa new species
Figures 348–353; Map 4

Holotype. Female holotype and male and two female paratypes from Curumim, Capão da Canoa, Rio Grande do Sul, Brazil, 18 Jan. 1978 (C. J. Becker, MCN no. 8128). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellowish with black marks (Fig. 350). Chelicerae yellowish with black patch on front. Labium, endites black. Sternum yellowish with median black patch. Coxae yellowish with black ring distally; legs yellowish with contrasting black rings. Dorsum of abdomen white and black (Fig. 350); venter with black mark anterior to spinnerets and two indistinct longitudinal white lines (Fig. 351). Posterior median eyes, anterior lateral eyes, posterior lateral eyes all 0.8 diameter of anterior median eyes. Anterior median eyes slightly less than one diameter apart; posterior median eyes 1.5 diameters apart. Abdomen oval, pointed behind with shoulder humps (Fig. 350). Total length 6.5 mm. Carapace 3.1 mm long, 2.1 wide. First femur 2.3 mm; patella and tibia 2.9; metatarsus 1.9; tarsus 1.1. Second patella and tibia 2.5 mm; third 1.7; fourth 2.7.

Male. Coloration as in female. Abdomen shorter than that of female (Fig. 352). Total length 5.9 mm. Carapace 3.2 mm long, 2.5 wide. First femur 2.7 mm; patella and tibia 3.2; metatarsus 1.8; tarsus 1.0. Second patella and tibia 2.6 mm; third 2.0; fourth 2.7.

Variation. Total length of females from 6.5 to 7.2 mm, of males from 5.6 to 5.9. The female holotype and male paratype from Rio Grande do Sul are illustrated and described.

Diagnosis. The female differs by having an angular lip in the epigynum and the median lobe with a seam (Fig. 348), the male has a small projecting median apophysis in the palpus, the terminal apophysis describing a half circle (Fig. 353).

Natural History. Specimens from Rio de Janeiro had the web near the ground, 10 cm diameter, on steep shaded roadside.

Paratypes. BRAZIL *Rio de Janeiro*: Paineiras on Corcovado Mtn., 30 Mar. 1983, ♀, 3 imm (H. L. Levi, MCZ). *Rio Grande do Sul*: Curumim, Capão da Canoa, 3 Nov. 1974, ♂ (C. J. Becker, MCN 2408).

Alpaida yuto new species
Figures 354–359; Map 4

Holotype. Female holotype and female paratype from Yuto, Jujuy Prov., Argentina, Nov. 1966 (M. E. Galiano, MACN no. 8455). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum orange. Coxae orange with dusky patches; legs contrastingly ringed orange and black. Dorsum of abdomen patterned (Fig. 356); sides black; venter with black patch surrounded by orange-white (Fig. 357). Secondary eyes 0.8 diameter of anterior median eyes. Anterior median eyes 0.6 diameter apart, posterior median eyes their diameter apart. Abdomen oval, pointed behind. Total length 7.8 mm. Carapace 3.4 mm long, 2.7 wide. First femur 3.1 mm; patella and tibia 3.7; metatarsus 2.5; tarsus 1.1. Second patella and tibia 3.1 mm; third 2.1; fourth 3.4.

Male. Coloration as in female (Fig. 358). Secondary eyes 0.8 diameter of anterior median eyes. Anterior median eyes and posterior medians each their diameter apart. Second tibia slightly thicker than first, with macrosetae. Fourth trochanters with one or two short macrosetae. Total length 6.4 mm. Carapace 3.1 mm long, 2.7 wide. First femur 3.1 mm; patella and tibia 3.8; metatarsus 2.3; tarsus 1.1. Second patella and tibia 2.9; third 2.1; fourth 3.2.

Variation. Total length of females from 5.9 to 8.7 mm, of males, 6.4 to 6.8. The specimens from the Chaco have black patches on the head.

The female holotype and male paratype from Jujuy Province are described and illustrated.

Diagnosis. Females differ from those of *A. canoa* by more rounded lips in ventral view of the epigynum (Fig. 354) and wider lips when viewed from posterior (Fig. 355). The males differ from those of *A. canoa* by having the embolus sickle-shaped, the median apophysis narrower and the edge of the terminal apophysis concave (Fig. 359).

Natural History. Kochalka (in letter) states that, like *A. itapua*, *A. yuto* is found in undisturbed forest among roots at the bases of trees. The small webs are a few inches above the ground and have a line going from the hub to a retreat in the substrate. The spider remains at the hub day and night and runs to the retreat when disturbed.

Records. PARAGUAY *Concepción*: Apa [Río Apa] 1909, ♀ (AMNH). *Chaco*: Parque Nac. Defensores del Chaco, 24–31 July 1983, 2♀, ♂ imm. (J. Kochalka, MNHNP, MCZ). ARGENTINA *Jujuy*: Yuto, El Pandanaso, Oct. 1967, ♂, March 1967, ♀ (M. E. Galiano, MACN 8456, 8457).

Alpaida weyrauchi new species
Figures 360–363; Map 4

Holotype. Female holotype, two female, one immature paratypes from Valle Chanchamayo, 800 m, Peru [11°35'S, 75°19'W, Dpto. Junín] 1 Feb. 1953 (W. K. Weyrauch, CAS, one paratype in MCZ). The species is named after the collector.

Description. Female. Carapace orange, head and middle of thorax black. Labium, endites, black. Sternum orange with median black streak and a black border. Coxae black; legs ringed black on orange. Dorsum of abdomen with cardiac mark with some white pigment and indistinct black pattern on orange (Fig. 362); venter with a pair of parallel light lines on black (Fig. 363). Secondary eyes 0.8 times diameter of anterior median eyes. Anterior median eyes their diameter apart; posterior me-

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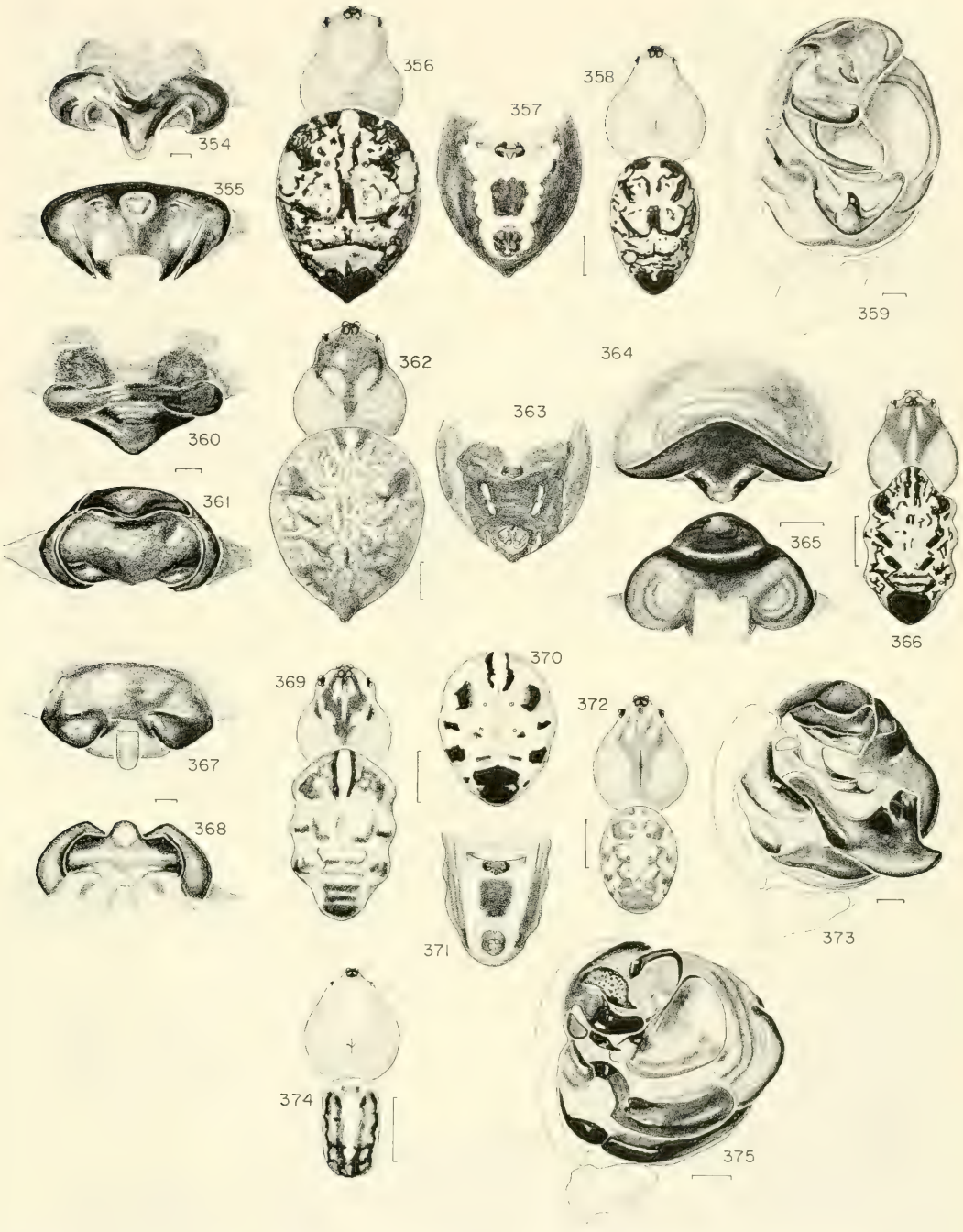
Figures 354–359. *Alpaida yuto* n. sp. 354–357, female. 354, epigynum, ventral. 355, epigynum, posterior. 356, dorsal. 357, ventral. 358, 359, male. 358, dorsal. 359, left palpus.

Figures 360–363. *A. weyrauchi* n. sp., female. 360, epigynum, ventral. 361, epigynum, posterior. 362, dorsal. 363, ventral.

Figures 364–366. *A. deborae* n. sp., female. 364, epigynum, ventral. 365, epigynum, posterior. 366, dorsal.



Figures 367–373. *A. lubinae* n. sp. 367–371, female. 367, epigynum, ventral. 368, epigynum, posterior. 369, 370, dorsal. 371, ventral. 372, 373, male. 372, dorsal. 373, palpus.

Figures 374–375. *A. yungas* n. sp., male. 374, dorsal. 375, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

dian eyes slightly less than their diameter apart. Abdomen oval, pointed behind (Fig. 362). Total length 7.7 mm. Carapace 3.7 mm long, 2.9 wide. First femur 3.5 mm; patella and tibia 4.1; metatarsus 2.6; tarsus 1.2. Second patella and tibia 3.6 mm; third 2.4; fourth 3.7.

Note. The holotype (Figs. 360–363) has a complete epigynum, the tip is torn off from two paratypes, the breaking point is visible in the intact epigynum.

Variation. Total length of females from 6.2 to 7.7 mm.

Diagnosis. Females differ from *A. deborae* by having the lips of the epigynum in a straight transverse line (Fig. 360).

Record. PERU *Junín*: San Ramón, 20 July 1965, ♀ (P. Wygodzinsky, AMNH).

Alpaida deborae new species
Figures 364–366; Map 4

Holotype. Female from Browns Berg, 5°N, 55°27′W, Brokopondo Prov., Surinam, 20 Feb. 1982, (D. Smith Trail, MCZ). The species is named after the collector.

Description. Female. Carapace yellow white with black head and black rim around thorax (Fig. 366). Labium, endites, sternum, black. Coxae, yellow-white; legs yellow white with black rings. Dorsum of abdomen with black chevrons and anterior median white line (Fig. 366); venter black. Abdomen with three pairs lateral humps. Total length 4.5 mm. Carapace 2.1 mm long, 1.5 wide. First femur 1.7 mm; patella and tibia 2.2; metatarsus 1.3; tarsus 0.8. Second patella and tibia 1.9 mm; third 1.2; fourth 2.0.

Note. A specimen of this species from Uassa [Uaça, Amapá, Brazil] was in the PAN collection marked *Singa guianensis* Tacz. However, the description of *Singa guianensis* does not fit the specimen so labeled.

Variation. All specimens measured 4.5 mm total length.

The holotype is described and illustrated.

Diagnosis. Females differ from those of *A. weyrauchi* by having the lips of the epigynum angled as a roof (Fig. 364) and having two sclerotized circles in posterior view (Fig. 365). As in *A. weyrauchi* the lobe has a seam where it tears off.

Paratypes. SURINAM *Brokopondo*: Browns Berg, 5°N, 55°27′W, 20 Feb. 1982, ♀ (D. Smith Trail, MCZ). FRENCH GUIANA St. Laurent de Maroni, ♀ (K. Jelski, PAN). BRAZIL *Pará*: Belém, Mocambo, Aug. 1970, ♀ (M. E. Galiano, MACN 8495).

Alpaida lubinae new species
Figures 367–373; Map 4

Holotype. Female from Rancho Grande, Prov. Aragua, Venezuela, June 1974 (Y. Lubin YDB 6,7,9, MCZ). The species is named after the collector.

Description. Female. Carapace orange yellow with black marks (Fig. 369). Labium, endites, black. Sternum yellowish with median black patch. Legs yellowish-white with narrow, black rings. Dorsum of abdomen mottled black with a white cardiac mark framed black (Fig. 369); sides black; venter with black square mark, light

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Figures 376–378. *Alpaida erythrothorax* (Taczanowski), female. 376, epigynum, ventral. 377, epigynum, posterior. 378, dorsal.

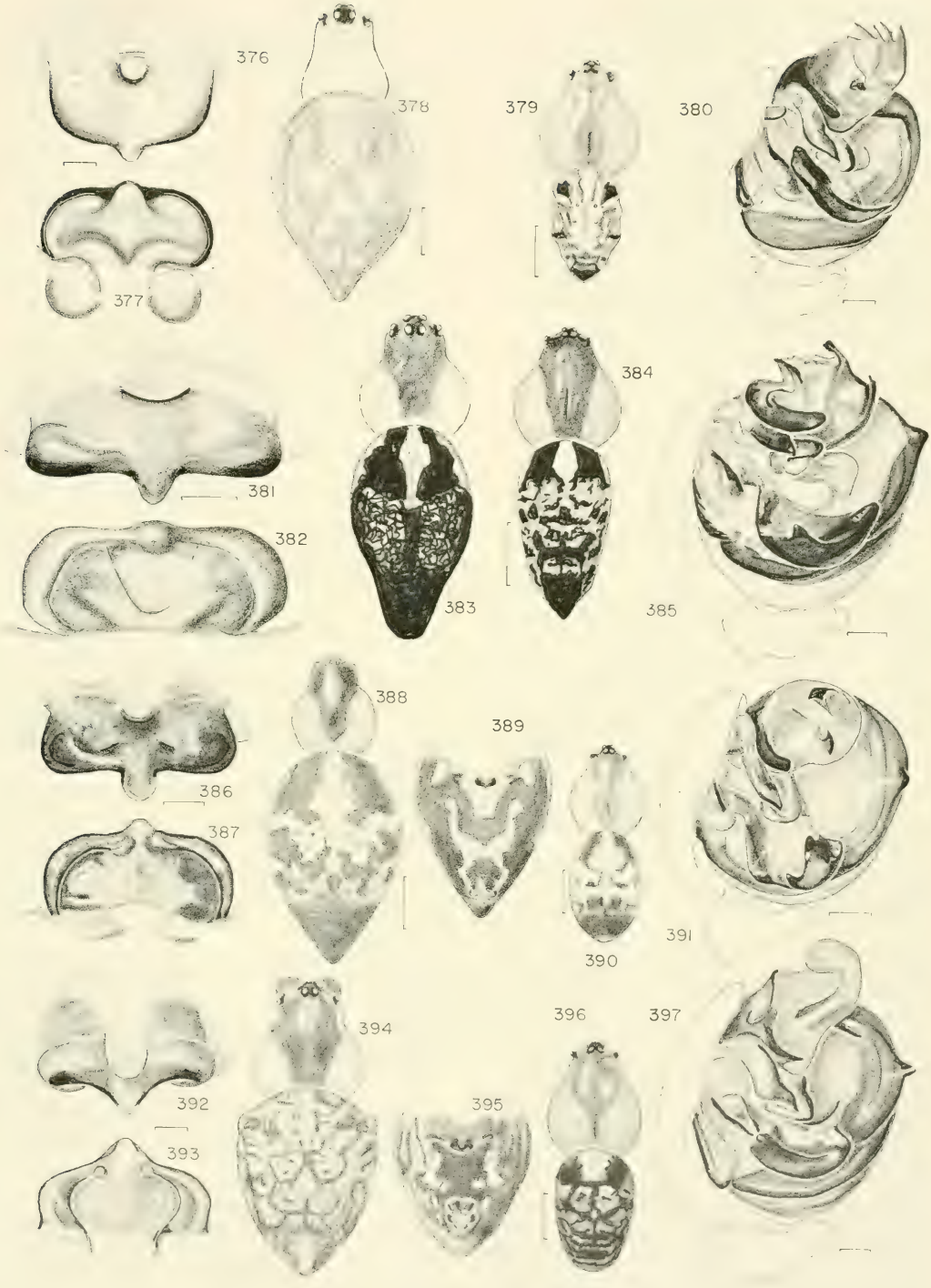
Figures 379, 380. *A. vera* n. sp., male. 379, dorsal. 380, left palpus.

Figures 381–385. *A. trilineata* (Taczanowski). 381–383, female. 381, epigynum, ventral. 382, epigynum, posterior. 383, dorsal. 384, 385, male. 384, dorsal. 385, palpus.

Figures 386–391. *A. itauba* n. sp. 386–389, female. 386, epigynum, ventral. 387, epigynum, posterior. 388, dorsal. 389, ventral. 390, 391, male. 390, dorsal. 391, palpus.

Figures 392–397. *A. antonio* n. sp. 392–395, female. 392, epigynum, ventral. 393, epigynum, posterior. 394, dorsal. 395, ventral. 396, 397, male. 396, dorsal. 397, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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on each side (Fig. 371). Abdomen of holotype has pairs of bulges on sides and is posteriorly pointed (Fig. 369). Total length 5.0 mm. Carapace 2.2 mm long, 1.9 wide. First femur 2.1 mm; patella and tibia 2.6; metatarsus 1.7; tarsus 0.9. Second patella and tibia 2.1 mm; third 1.4; fourth 2.3.

Male. Coloration as in female (Fig. 372). Eyes as in female. Second tibiae slightly thicker than first with macrosetae. Total length 4.1 mm. Carapace 2.3 mm long, 1.8 wide. First femur 2.2 mm; patella and tibia 2.7; metatarsus 1.5; tarsus 0.7. Second patella and tibia 1.9 mm; third 1.4; fourth 2.0.

Variation. Total length of females from 4.5 to 5.6 mm, males from 3.6 to 4.5. The abdomen of females may be oval with slight shoulder humps and pointed behind (Fig. 370) or when emaciated as in Figure 369.

The holotype is described and illustrated.

Diagnosis. Females distinguished by the median lobe of the epigynum, which is set off with parallel sides (Fig. 367) and has swollen lips. The median apophysis of the palpus projects to the side and the terminal apophysis is subtriangular (Fig. 373).

Paratypes. VENEZUELA *Mérida*: Mérida, July 1974, 2♀ (A. L. Edgar, MCZ). *Aragua*: Rancho Grande, many ♀♀, ♂♂ (AMNH, MACN 8469, MCZ).

Alpaida yungas new species
Figures 374, 375; Map 4

Holotype. Male from Chulumani, 1,700 m, Yungas, Dpto. La Paz, Bolivia, 17–25 Dec. 1955 (L. Peña, IRSNB). The specific name is a noun in apposition after the locality.

Description. Male. Carapace yellow. Sternum, endites black. Coxae, legs yellow, distal articles brown. Dorsum of abdomen with median white band, sides yellowish with two black bands on each side (Fig. 374); venter black with an indistinct light longitudinal line on each side surrounding spinnerets posteriorly. Anterior median eyes slightly less than their diameter apart; posterior medians their diameter apart. Second tibiae slightly thicker than first. Total length 3.4 mm. Carapace 1.7 mm long, 1.5 wide. First femur 1.8 mm; patella and tibia 1.9; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.5 mm; third 0.9; fourth 1.4.

Diagnosis. This male differs from others by the short, stubby embolus, the long curved median apophysis with parallel sides, the heavy basal prong of the terminal apophysis, and the large conductor of the palpus (Fig. 375).

Alpaida erythrothorax (Taczanowski), new combination
Figures 376–378; Map 4

Singa erythrothorax Taczanowski, 1873: 126. Female lectotype, 2 male and 1 juvenile paralectotypes from Cayenne, French Guiana (PAN), examined. The male paralectotypes are *A. leucogramma*. Roewer, 1942: 877.

Araneus erythrothorax:—Bonnet, 1955: 501.

Description. Female. Carapace orange. Sternum with white pigment. Coxae light orange, legs gray, first femora light on sides. Dorsum of abdomen with uneven gray pigment and a median longitudinal white band, and a white longitudinal band on each side (Fig. 378); venter between epigynum and spinnerets with a black spot in center and white pigment on each side; white pigment continuous with pigment posterior to spinnerets underneath overhang. Posterior median eyes about 1.4 diameters of anterior medians, laterals about 0.8 diameter. Anterior medians less than their diameter apart, posterior medians more than their diameter apart. Fourth legs slightly longer than first. Total length 5.8 mm. Carapace 2.4 mm long, 2.3 wide. First patella and tibia 2.4 mm; second 2.2; third 1.6. Fourth femur 2.1 mm; patella and tibia 2.4; metatarsus 1.6; tarsus 0.9.

Diagnosis. Unlike that of *A. trilineata*, the median notch is more than twice its diameter from the posterior margin of the epigynum (Fig. 376).

Alpaida vera new species
Figures 379, 380; Map 4

Holotype. Male from Vila Vera, 55°30'W, 12°46'S, Mato Grosso, Brazil, Oct. 1973 (M. Alvarenga, AMNH). The specific name is a noun in apposition after the locality.

Description. Male. Carapace orange with median brown band; band branches and fades anteriorly on head. Sternum orange with median dark mark. Coxae orange; legs ringed contrasting brown on orange. Dorsum of abdomen with white cardiac mark, black shoulder patches and black posterior tip, and black pattern on dusky orange (Fig. 379); venter black, orange longitudinal band on each side. Median eyes slightly less than their diameter apart. Second tibiae the same thickness as first. Fourth trochanters with two small macrosetae. Abdomen oval with shoulder humps and posterior tip. Total length 4.5 mm. Carapace 2.4 mm long, 1.9 wide. First femur 2.2 mm; patella and tibia 2.6; metatarsus 1.7; tarsus 0.8. Second patella and tibia 2.1 mm; third 1.5; fourth 2.2.

Diagnosis. The projecting terminal apophysis of the palpus with five fingers (Fig. 380) separates this species from similar species.

Alpaida trilineata (Taczanowski), new combination
Figures 381–385; Map 4

Epeira trilineata Taczanowski, 1878: 162, pl. 2, fig. 13, ♀. Female lectotype and one female paralectotype here designated from Amable María [640 m, Dpto. Junín, prov. Tarma], Peru (PAN), examined.

Aranea trisignata Roewer, 1942: 854. New name for *Epeira trilineata* Taczanowski, 1878, thought preoccupied by *Aranea trilineata* Linnaeus, 1767. NEW SYNONYMY.

Araneus trilineatus:—Bonnet, 1955: 618.

Description. Female. Carapace yellow-white with a longitudinal black band which covers head. Distal half of chelicerae black. Sternum, coxae yellow-white. Legs ringed. Dorsum of abdomen with black and white pattern (Fig. 383); sides black; venter yellow-white with black marks between epigynum and spinnerets, and some white pigment spots on each side of the median black area. Posterior median eyes 1.2 diameters; laterals 0.8 diameter of anterior median eyes. Abdomen pointed behind (Fig. 383). Fourth legs longer than first. Total length 4.3 mm. Carapace 1.8 mm long, 1.5 wide. First patella and tibia 2.1 mm; second 1.7; third 1.4. Fourth femur 1.6 mm; patella and tibia 2.1; metatarsus 2.0; tarsus 0.6.

Male. Coloration and eye sizes as in female (Fig. 384), except first three pairs of coxae black. Second tibiae as thick as first and with macrosetae. Abdomen oval, pointed behind, with distinct shoulder humps. Total length 4.5 mm. Carapace 2.1 mm long, 1.6 wide. First femur 1.9 mm; patella and tibia 2.2; metatarsus 1.2; tarsus 0.6. Second patella and tibia 1.7; third 1.4; fourth 2.1.

Note. The paralectotype is much lighter in color; it seems to be the same species as the lectotype.

Diagnosis. Females are distinguished from those of *A. erythrothorax* and *A. itauba* by the wide notch of the epigynum, which lies a distance equal to its width from the posterior edge (Fig. 381). The males are distinguished from those of *A. itauba* by a longer median apophysis in the palpus, a "horizontally" curved basal prong of the terminal apophysis, and a distal frayed edge (Fig. 385).

Record. PERU *Junín*: San Ramón, 20–27 July 1965, ♂, (P. B. Wygodzinsky, AMNH).

Alpaida itauba new species
Figures 386–391; Map 4

Holotype. Female from Itaúba, Arroio do Tigre, Rio Grande do Sul, Brazil, 10 April 1978 (C. J. Becker, MCN no. 7909). The specific name is a noun in apposition after the locality.

Description. Female. Carapace black, sides yellowish. Chelicerae, labium, endites black. Sternum yellowish with white pigment spots. Legs yellowish with narrow black rings; coxae black, fourth mostly yellowish. Dorsum of abdomen with white cardiac mark, black marks, posterior black (Fig. 388); venter marked black on yellowish (Fig. 389); spinnerets black. Anterior median eyes, lateral eyes, subequal; posterior median eyes 1.4 diameters of the others. Anterior median eyes, posterior median eyes slightly more than their diameters apart. Fourth legs longer than first. Abdomen pointed behind. Total length 5.8

mm. Carapace 1.9 mm long, 1.5 wide. First femur 1.5 mm; patella and tibia 1.9; metatarsus 1.3; tarsus 0.7. Second patella and tibia 1.7 mm; third 1.4; fourth 2.1.

Male. Coloration as in female (Fig. 390); venter of abdomen mostly light colored. Total length 3.9 mm. Carapace 1.9 mm long, 1.5 wide. First femur 1.9 mm; patella and tibia 2.1; metatarsus 1.4; tarsus 0.7. Second patella and tibia 1.5 mm; third 1.3; fourth 2.0.

Variation. Females vary in total length from 4.7 to 5.8 mm.

The female holotype and a male from Rio Grande do Sul (MCN) are described and illustrated.

Diagnosis. Females distinguished from those of *A. erythrothorax* by the black head and the larger, rounded sides of the epigynum (Fig. 386). Males distinguished from others by the shorter median apophysis and the "vertical" curved, basal prong and undivided distal margin of the terminal apophysis (Fig. 391).

Paratypes. BRAZIL *São Paulo*: Piraçununga, 16 May 1940, ♀ (Schubart, MZSP 6467); Morro do Serrote, Juguiá, 16 Nov. 1952, ♀ (Schubart, MZSP 4980). *Rio Grande do Sul*: Itaúba, Arroio de Tigre, 6 Apr. 1978, ♀ (E. M. Buckup, MCN 7830); 8 Apr. 1978, ♂ (H. Bischoff, MCN 7871). ARGENTINA *Salta*: Vada Hondo, Orán, Mar. 1967, ♂ (M. E. Galiano, MACN 8459).

Alpaida antonio new species
Figures 392–397; Map 4

Holotype. Female from Fazenda Santo Antonio, Uruçuca, Bahia, Brazil, 27 Nov. 1977 (J. S. Santos, MCN no. 11012). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange with black marks. Labium, chelicerae, endites black. Sternum light orange. Coxae dusky black; legs light orange with black rings. Dorsum of abdomen dark with indistinct folium (Fig. 394); venter with a pair of white marks on dark background (Fig. 395). Anterior median eyes and posterior median eyes each slightly less than their diameter apart. Abdomen with some hairs, lightly sclerotized shoulder humps, and posterior point (Fig. 394). Total length 6.4 mm. Carapace 2.8 mm long, 2.1 wide. First femur 2.7 mm; patella and tibia 3.1; metatarsus 2.0; tarsus 0.9. Second patella and tibia 2.6 mm; third 1.8; fourth 2.8.

Male. Coloration as in female (Fig. 396), except sternum with median black line. Anterior median eyes 0.6 their diameter apart; posterior median eyes 0.8 their diameter apart. Second tibiae thicker than first with macrosetae. Total length 5.0 mm. Carapace 2.9 mm long, 2.3 wide. First femur 2.9 mm; patella and tibia 3.4; metatarsus 2.0; tarsus 1.0. Second patella and tibia 2.5 mm; third 2.0; fourth 2.9.

Note. Males and females were matched because of color and size. The female holotype and a male from Canindé (AMNH) are described and illustrated.

Variation. Total length of females varies from 5.9 to 6.4 mm, males from 4.7 to 5.6.

Diagnosis. Females differ from those of *A. itauba* by having the posterior tip of the notch in line with the posterior margin of the epigynum and the anterior margins of the lips on each side parallel with the posterior margins (Fig. 392), and the posterior median plate narrower (Fig. 393). Males differ from similar species in having a tooth instead of the basal prong on the terminal apophysis in the palpus and having the terminal apophysis' distal and drawn out and bent "forward" (Fig. 397).

Paratypes. GUYANA *Bartica Distr.*: Kartabo, Nov. 1920, ♂ (AMNH). BRAZIL *Pará*: 59 km E of Canindé, May 1963, ♂ (B. Malkin, AMNH); Canindé, Rio Gurupi, 17 Dec. 1964, ♀ (B. Malkin, AMNH). *Bahia*: Fazenda Matiapa, Camacã, 16 Oct. 1979, ♀ (J. S. Santos, MCN 10861). *Espírito Santo*: Rio São José, 24 Sept. 1942, ♂ (H. Soares, MZSP 8031).

Alpaida niveosagillata (Mello-Leitão)
Figures 398–403; Map 4

Singa niveosagillata Mello-Leitão, 1941a: 260, fig. 1, ♀. Female holotype from Sasaima, [Dpto. Cundinamarca] Colombia (MNRJ), examined.

Alpaida niveosagillata:—Brignoli, 1983: 256. Eberhard, 1986, 73, fig. 4.2h (web).

Description. Female. Carapace yellow-white with dark marks; labium, endites, and sternum black; coxae yellow-white with a black patch; legs with black and yellowish rings of equal width. Dorsum of abdomen black and gray with anterior median and lateral white marks (Fig. 400); venter black with a pair of white patches, also, a white spot on each side of the spinnerets (Fig. 401). Abdomen oval with a posterior tubercle (Fig. 400). Total length 5.0 mm. Carapace 2.2 mm long, 1.7 wide. First femur 1.5 mm; patella and tibia 2.3; metatarsus 1.3; tarsus 0.5. Second patella and tibia 1.8 mm; third 1.1; fourth 2.0.

Male. Coloration as in female (Fig. 402). Total length 3.5 mm. Carapace 1.8 mm long, 1.5 wide. First femur 1.8 mm; patella and tibia 2.3; metatarsus 1.1; tarsus 0.8. Second patella and tibia 1.7 mm; third 1.2; fourth 1.8.

Note. Female and male have not been collected together but are matched because of similar markings.

Variation. Total length of females from 5.0 to 6.5 mm, of males from 3.5 to 4.2. A female from Dpto. Valle (MCZ) and male from Dpto. Cauca (MCZ) are described and illustrated.

Diagnosis. Females can be distinguished from all other *Alpaida* by the strongly curved lips in ventral view of the epigynum. The lips are parallel in the midline (Fig. 398). The male palpus has a sword-shaped embolus, a median apophysis with a large pointed lobe and a complexly folded terminal apophysis (Fig. 403).

Natural History. The web has been illustrated by Eberhard (1986).

Records. COLOMBIA *Valle*: 50 km S of Buenaventura, 50 m, Mar. 1973, imm., ♀ (W. Eberhard I-504, MCZ); Lago Calima, between Buga and Loboguerrero, Sept. 1973, ♀ (W. Eberhard, MCZ). *Cauca*: Pacific coastal plain, NW of Guapi, Jan. 1973, ♂ (W. Eberhard, MCZ). ECUADOR *Pichincha*: 35 km NW of Santo Domingo de los Colorados, ♂ (A. M. Nadler, AMNH). *El Oro*: Buena Vista, 25 km SE Machala, ♀ (R. Walls, CAS).

Alpaida rossi new species
Figures 404–407; Map 4

Holotype. Female from Monzón Valley, Tingo María, Dpto. Huánuco, Peru, 10 Nov. 1954 (E. I. Schlinger and E. S. Ross, CAS). This species is named after the collector.

Description. Female. Carapace orange with black marks. Sternum dark brown. Coxae orange; legs orange with narrow black rings. Dorsum of abdomen with white cardiac mark on mottled brown-to-black (Fig. 406); venter black with white pigment in light area on each side (Fig. 407). Abdomen with distinct shoulder humps, slight humps on sides, and posterior pointed tip (Fig. 406). Total length 5.9 mm. Carapace 2.6 mm long, 2.0 wide. First femur 2.3 mm; patella and tibia 2.7; metatarsus 1.8; tarsus 0.9. Second patella and tibia 2.4 mm; third 1.7; fourth 2.5.

Variation. Total length of females varies from 5.9 to 6.7 mm.

The holotype is described and illustrated.

Diagnosis. The median lobe of the epigynum, unlike others, is constricted at its base and the lips are swollen toward the median (Fig. 404).

Paratypes. PERU *Huánuco*: Tingo María, 8 Oct. 1946, ♀ (J. C. Pallister, AMNH). *Ucayali*: Colonia Calleria, Río Calleria, 15 km from Ucayali, Oct. 1961, ♀ (B. Malkin, AMNH).

Alpaida boa new species
Figures 408, 409; Map 4

Holotype. Male from Fonte Boa, Amazonas, Brazil, Sept. 1975 (M. Oliveira, AMNH). The specific name is a noun in apposition after the locality.

Note. The holotype is in poor physical condition.

Description. Male. Carapace orange with head, middle of thorax, and edge of thorax black. Labium, sternum, endites black. Coxae orange; proximal half of femora orange, distal black, distal articles con-

trastingly ringed black on orange. Dorsum of abdomen with white cardiac mark and indistinct mottled black folium on dusky orange (Fig. 408); venter black, sides dusky orange. Anterior median eyes slightly more than their diameter apart; posterior median eyes their diameter apart. Second tibiae same diameter as first with macrosetae. Total length 3.5 mm. Carapace 1.8 mm long, 1.5 wide. First femur 1.8 mm; patella and tibia 2.1; metatarsus 1.4; tarsus 0.7. Second patella and tibia 1.8 mm; third 1.2; fourth 2.0.

Diagnosis. This male differs from others by the long embolus, lobed median apophysis and large tegulum in the palpus (Fig. 409).

Alpaida negro new species
Figures 410–414; Map 4

Holotype. Female from Rio Negro, Est. Paraná, Brazil (Z. Rolas, MNRJ no. 58419). The specific name is a noun in apposition after the locality.

Description. Female. Carapace black, orange only on sides of thorax (Fig. 412). Labium, endites black; chelicerae black, dark orange distally. Sternum orange with black border and median black mark. Coxae black, fourth with yellow; legs ringed black and orange, black bands wider than orange. Dorsum of abdomen black and white (Fig. 412); venter black with a pair of white marks. Posterior median eyes 0.8 diameter of anterior medians; lateral eyes 0.7 diameter. Anterior median eyes 0.7 their diameter apart; posterior median eyes their diameter apart. Abdomen oval, pointed behind. Total length 7.9 mm. Carapace 3.1 mm long, 2.4 wide. First femur 2.8 mm; patella and tibia 3.6; metatarsus 2.3; tarsus 1.0. Second patella and tibia 2.9 mm; third 2.0; fourth 3.1.

Male. Coloration as in female. Eye sizes as in female. Anterior median eyes and posterior median eyes each 0.6 times their diameter apart. Second tibiae thicker than first, with a few macrosetae. Total length 7.8 mm. Carapace 4.1 mm long, 3.4 wide. First femur 4.1 mm; patella and tibia 5.1; metatarsus 2.9; tarsus 1.3. Second patella and tibia 3.9 mm; third 3.0; fourth 4.5.

Note. Males are larger than females.

Diagnosis. Females are distinguished from *A. moata* by a more rounded lobe on the epigynum (Fig. 410) and a transverse groove on the median plate (Fig. 411). Males distinguished by a wider median apophysis, a more slender embolus, and the unique folds of the terminal apophysis (Fig. 414). The heads of *A. negro* are black, those of *A. moata* orange.

Paratypes. BRAZIL *Mato Grosso*: [no locality] Oct. 1976, ♀, 2♂ (M. Alvarenga, AMNH).

Alpaida moata (Chamberlin and Ivie), new combination
Plate 2; Figures 415–420; Map 4

Araneus moatus Chamberlin and Ivie, 1936: 47, pl. 14, fig. 125. ♀. Female holotype from Barro Colorado Island, Panama (AMNH) examined. Bonnet, 1955: 545.

Aranea moata:—Roewer, 1942: 847.

Description. Female. Carapace, light orange, area of median eyes black. Chelicera, orange proximally, black distally.

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Figures 398–403. *Alpaida niveosagillata* (Mello-Leitão). 398–401, female. 398, epigynum, ventral. 399, epigynum, posterior. 400, dorsal. 401, ventral. 402, 403, male. 402, dorsal. 403, left palpus.

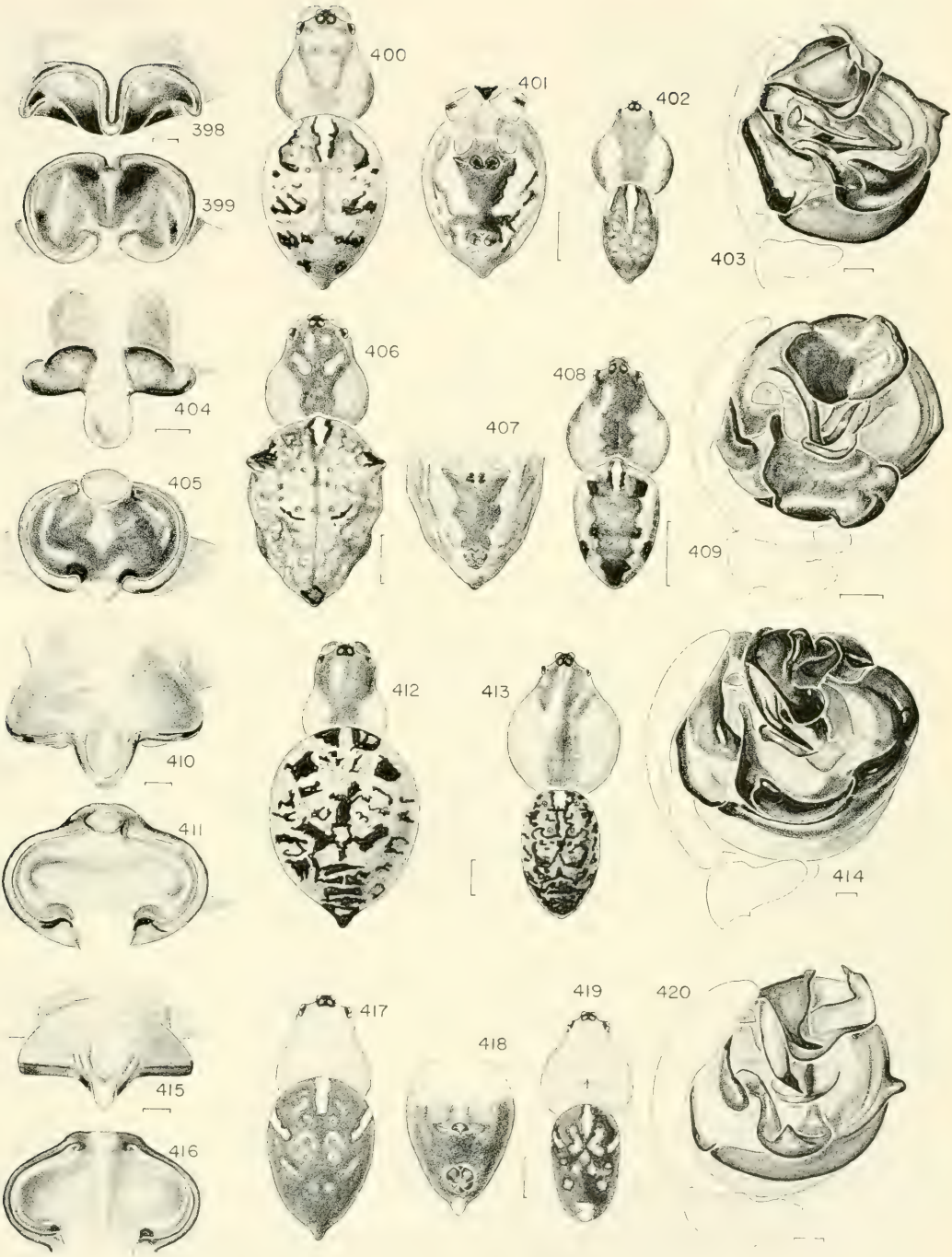
Figures 404–407. *A. rossi* n. sp., female. 404, epigynum, ventral. 405, epigynum, posterior. 406, dorsal. 407, ventral.

Figures 408, 409. *A. boa* n. sp., male. 408, dorsal. 409, palpus.

Figures 410–414. *A. negro* n. sp., 410–412, female. 410, epigynum, ventral. 411, epigynum, posterior. 412, dorsal. 413–414, male. 413, dorsal. 414, palpus.

Figures 415–420. *A. moata* (Chamberlin and Ivie). 415–418, female. 415, epigynum, ventral. 416, epigynum, posterior. 417, dorsal. 418, ventral. 419, 420, male. 419, dorsal. 420, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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Sternum, orange with small, median black streak; coxae, orange; legs, black. Dorsum of abdomen, black with anterior median light mark and paired indistinct white patches (Fig. 417); venter, black; book lung covers, brown. Abdomen oval, pointed posteriorly above spinnerets (Fig. 417). Total length 6.2 mm. Carapace 3.1 mm long, 2.1 wide. First femur 2.9 mm; patella and tibia 3.5; metatarsus 2.2; tarsus 1.1. Second patella and tibia 2.9 mm; third 2.0; fourth 3.1.

Male. Coloration as in female (Fig. 419). Total length 4.8 mm. Carapace 2.7 mm long, 2.1 wide. First femur 2.5 mm; patella and tibia 3.1; metatarsus 1.8; tarsus 1.0. Second patella and tibia 2.3 mm; third 1.7; fourth 2.6.

Variation. Total length of females from 6.1 to 6.9 mm, males from 4.5 to 5.1. Females from Colombia have the head and coxae black, the sternum orange with a black patch and a pair of white spots on the venter of the abdomen.

A male and female from Gamboa, Panama (MCZ) are described and illustrated.

Diagnosis. Unlike *A. negro*, the epigynum has a more pointed median lobe (Fig. 415) and a dorsoventral median ridge on the posterior median plate (Fig. 416). The male differs by having a narrower median apophysis, a round hump on the edge of the tegulum and a distal finger on the terminal apophysis (Fig. 420). The species is smaller than the sympatric *A. acuta*.

Records. PANAMA *Bocas del Toro*: Río Changuinola, Corriente Grande, 13–17 Mar. 1980, ♀ (R. Ibanez, MCZ). *Panamá*: El Valle, July 1936, ♂ (AMC); Gamboa, July 1981, ♂, ♀ (W. Eberhard 2215, MCZ); Barro Colorado Island, Lago Gatun, common (MCZ); Forest Reserve, 1939, ♂, 25 July 1954, ♂ (A. M. Chickering, MCZ). COLOMBIA *Valle*: Cisneros, Apr. 1976, ♀ (W. Eberhard 1086, MCZ); Anchicayá, Oct. 1975, ♀ (W. Eberhard 983, MCZ), 26 Oct. 1969, ♂ (W. Eberhard I-75, MCZ), Nov. 1973, ♂, ♀ (W. Eberhard, MCZ); 1975, ♂, (W. Eberhard, MCZ).

Alpaida acuta (Keyserling), new combination

Plate 2; Figures 421–426; Map 4

Epeira acuta Keyserling, 1865: 816, pl. 18, fig. 13, 14, ♀. Female holotype from New Granada [Spanish colony of Panama and Colombia] (BMNH), examined. Keyserling, 1893: 228, pl. 11, fig. 169, ♀.

Epeira rhodomelas Taczanowski, 1878: 147, pl. 1, fig. 3, ♀. Numerous syntypes from wasp nests from Amable María, Montana de Vitoc, [Dpto. Junín] Peru (PAN), examined. NEW SYNONYMY.

Aranea acuta:—Roewer, 1942: 836.

Aranea rhodomelas:—Roewer, 1942: 851.

Araneus acutus:—Bonnet, 1955: 420.

Araneus rhodomelas:—Bonnet, 1955: 586.

Note: Keyserling's single specimen has an all orange carapace.

Description. Female from Colombia. Carapace black, sides and posterior of carapace orange. Chelicerae, labium, endites black. Sternum orange. Legs black except coxae, trochanter and proximal ends of femora orange. Abdomen black with median ventral white spot (Fig. 424). Abdomen oval, pointed behind, with small anterior median hump (Fig. 423). Total length 9.4 mm. Carapace 3.5 long, 2.8 wide. First femur 2.6 mm; patella and tibia 3.1; metatarsus 1.9; tarsus 0.9. Second patella and tibia 2.8 mm; third 1.9; fourth 2.7.

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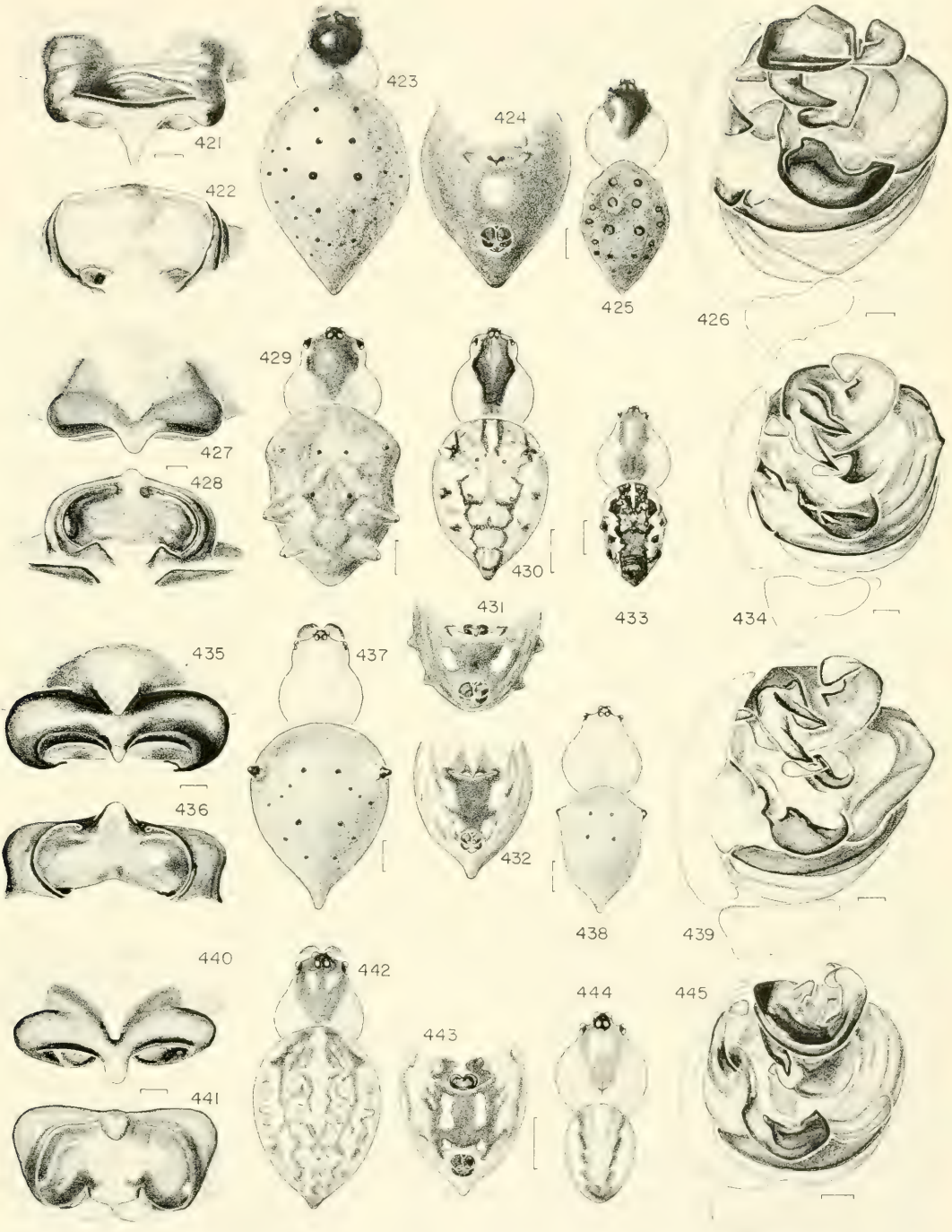
Figures 421–426. *Alpaida acuta* (Keyserling). 421–424, female. 421, epigynum, ventral. 422, epigynum, posterior. 423, dorsal. 424, ventral. 425, 426, male. 425, dorsal. 426, left palpus.

Figures 427–434. *A. septemmammata* (O. P.-Cambridge). 427–432, female. 427, epigynum, ventral. 428, epigynum, posterior. 429, 430, dorsal. 431, 432, ventral. 429, 431, (Dpt. Valle, Colombia). 430, 432, (Costa Rica). 433, 434, male. 433, dorsal. 434, palpus.

Figures 435–439. *A. graphica* (O.P.-Cambridge). 435–437, female. 435, epigynum, ventral. 436, epigynum, posterior. 437, dorsal. 438, 439, male. 438, dorsal. 439, palpus.



Figures 440–445. *A. urucuca* n. sp. 440–443, female. 440, epigynum, ventral. 441, epigynum, posterior. 442, dorsal. 443, ventral. 444, 445, male. 444, dorsal. 445, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

Male from Colombia. Coloration as in female (Fig. 425). Structure as in female, except second tibiae thicker than first and with microsetae. Total length 7.4 mm. Carapace 3.4 long, 2.7 wide. First femur 2.7 mm; patella and tibia 3.4; metatarsus 2.0; tarsus 0.9. Second patella and tibia 2.7 mm; third 1.8; fourth 2.6.

Variation. Total length of females 9.0 to 12.5 mm, males 5.8 to 7.7. Panamanian specimens are the smallest, have yellow heads, and may lack the light ventral spot.

A female and a male from Puerto Lopez, Colombia, are described and illustrated.

Diagnosis. Most specimens can be separated by the coloration, the black head (Fig. 423) and white ventral spot on the abdomen (Fig. 424), and the large size. Females can be separated from those of *A. septemmammata* by the straight anterior edge of the lip of the epigynum (Fig. 421); males by the larger median apophysis and straight basal prong of the terminal apophysis of the palpus (Fig. 426).

Natural History and Distribution. The web (Plate 2) was made on a recently felled tree trunk; others on the same trunk had almost no mesh near the orb. The species is found in wet lowland forest from Panama to northern Argentina (Map 4).

Records. PANAMA *Panamá*: Canal area (common) (AMNH, MCZ). COLOMBIA *Magdalena*: Río Cordua, Sierra Madre de Santa Marta, 750 m (MNHNP); San Pablo, San Pedro, 670 m (MNHNP). *Santander*: Río Opón, 1,000 m (AMNH); Río Suárez, 800–1,000 m (AMNH, MCZ). *Boyacá*: Río Upia, 850–950 (AMNH); Muzo (MCZ). *Meta*: 15 km SW Puerto López, 200 m (MCZ). ECUADOR *Napo*: Limóncocha, 240 m (MCZ, MECN). *Pastaza*: 11 km W Mera (CAS). *Morona-Santiago*: nr. General Plaza (Limón) (MCZ). PERU *Loreto*: Boquerón, 470 m (AMNH). *San Martín*: Hara, 32 km SE Moyobamba (AMNH). *Huánuco*: Tingo María, 670 m (AMNH); 69 km E Tingo María (CAS); Cord Azul, 1,400 m (AMNH). *Cuzco*: Chanchosmayo Valley (AMNH). BRAZIL *Amazonas*: Manaus (MCZ). BOLIVIA *Santa Cruz*: Sara (MCZ). *Cochabamba*: Chapare, Río Chipiriri (IRSNB). ARGENTINA *Misiones*: Puerto Victoria (MNRJ).

Alpaida septemmammata (O. P.-Cambridge), new combination
Figures 427–434; Map 4

Epeira septemmammata O. P.-Cambridge, 1889: 42, pl. 7, fig. 6, ♀. Fifteen specimens from Teapa, Mexico (BMNH) examined, but type recorded as coming from Choctum, Guatemala, not located. Keyserling, 1892: 89. pl. 4, fig. 67, ♀.

Aranea septemmammata:—F. P.-Cambridge, 1904: 514, pl. 49, fig. 15, ♀. Roewer, 1942: 852.

Araneus septemammatus:—Bonnet, 1955: 593.

Description. Female from Colombia. Carapace orange-yellow and brownish black. Chelicerae dark brown. Labium, endites black; sternum orange. Coxae black; legs black with yellow patches or rings. Dorsum of abdomen brownish black with indistinct pattern (Fig. 429); venter with one pair of white patches (Fig. 431). Abdomen with seven humps, covered by short hair (Fig. 429). Total length 7.4 mm. Carapace, 3.5 mm long, 2.9 wide. First femur 3.4 mm; patella and tibia 4.4, metatarsus 2.7; tarsus 1.1. Second patella and tibia 3.5 mm; third 2.5; fourth 3.5.

Male from Belize. Coloration as in female, but abdomen with more distinct pattern (Fig. 433); legs ringed. Second tibiae thicker than others. Abdomen with three pairs of lateral humps, anterior pair most dorsal. Total length 5.2 mm. Carapace, 2.5 mm long, 2.0 wide. First femur 2.2 mm; patella and tibia 2.5; metatarsus 1.5; tarsus 0.7. Second patella and tibia 2.0 mm; third 1.5; fourth 2.3.

Note. The sexes have been matched because of coloration and abdomen shape.

Variation. Total length of females from 4.9 to 8.1 mm, males from 3.6 to 5.5. The largest come from Argentina. Females may have pairs of large tubercles on the sides of the abdomen (Fig. 429), or may just have shoulder humps (Fig. 430). Some specimens have light coxae. Argentine fe-

males had only one pair of shoulder humps and the median apophysis of the palpus was proportionally slightly larger.

Figures 427 to 429 and the description are made from a female from Cali, Colombia (MCZ). The male illustrated and described came from Belize (MCZ).

Diagnosis. The posterior edge of the epigynum is nearly straight and has swollen lips, most pronounced on the sides (Fig. 427); the posterior median plate is oval (Fig. 428). The basal prong of the terminal apophysis on the palpus is pointed, with the distal lobe hanging over; the tegulum has a small lateral tubercle and the median apophysis is small (Fig. 434). The head is black, the sternum orange. While these characters separate the species from others in the northern part of the range, separation becomes difficult in South America with many similar species.

Records. MEXICO *Veracruz*: 0.5 km N of Sontecomapan, 21 Aug. 1967, ♀ (R. E. Leech, REL). *Chiapas*: Las Ruinas Palenque, July 1948, ♀ (C. Goodnight, AMNH). BELIZE 80 km S of Stann Creek, 2 June 1975, ♂ (W. Sedgwick, MCZ). COSTA RICA *Puntarenas*: Reserva Biologica Carara nr. Tárcoles, 28 July 1983, ♀ (H., L. Levi, W. Eberhard, MCZ); Corcovado-Sirena, Feb. 1984, ♂, Mar. 1984, 4♀ (W. Eberhard, MCZ). PANAMA *Veraguas*: Alto Limón Lo Yegueda, 11 Aug. 1984, ♀ (D. Quintero, MIUP). *Panamá*: Barro Colorado Island, Oct. 1975, ♀ (W. Eberhard, E-159, MCZ); France Field, Aug. 1973, ♂ (A. M. Chickering, MCZ); Villa Darién, Feb. 1984, 2♀ (M. N. García, MUIP). *Colón*: Guayabalito, Gatuncillo, Chagres River, 17 Aug. 1945, ♀ (E. Fichter, AMNH);

TRINIDAD Gasparee, Nov. 1944, ♀ (G. Donald, AMNH). VENEZUELA *Carabobo*: San Esteban, 26 Jan. 1940, ♂ (P. Andruze, AMNH). COLOMBIA *Magdalena*: San Pedro, Sierra Nevada de Santa Marta, 960 m, 19 May 1975, ♀ (J. A. Kochalka, MNHNP). *Valle*: nr. Cisneros, 500 m, Apr. 1976, ♀ (W. Eberhard 1092, MCZ); Queremal, 1,600 m, Aug. 1977, 6♀ (W. Eberhard E226, 1196, MCZ); Río Tuluá, 1,100 m, Aug. 1977, 2♀ (W. Eberhard, 1198, 1212, MCZ). ECUADOR *Pastaza*: 4.5 km N Puyo, 953 m, 9 Feb. 1955, ♀ (E. I. Schlinger, E. S. Ross, CAS). *Morona-Santiago*: Las Troyos, 29 July 1926, ♀ (MCZ). ARGENTINA *Misiones*: Gruta India, Ruta 12 Oct. 1977, 3♂, 2♀ (M. E. Galiano, MEG); Parque Nac. Iguazu, Oct. 1977, ♀ (M. E. Galiano, MEG).

Alpaida graphica (O. P.-Cambridge), new combination

Plate 1; Figures 435–439; Map 4

Epeira graphica O. P.-Cambridge, 1889: 22, pl. 7, fig. 16, ♂. Male holotype from Bugaba [22 km NW David, Chiriquí], Panama (BMNH), examined. Keyserling, 1892: 121, pl. 6, fig. 89, ♂.

Aranea graphica:—F. P.-Cambridge, 1904: 518, pl. 51, fig. 2, ♂. Roewer, 1942: 843.

Araneus graphicus:—Bonnet, 1955.

Note. Epeira graphica of O. P.-Cambridge, 1889: pl. 7, fig. 16 and Keyserling, 1892, are not this species but are *A. acuta*. However, F. P.-Cambridge, 1904: 518, pl. 51, fig. 2, ♂ is this species.

Description. Female. Carapace, sternum orange. Chelicerae orange, black distally. Coxae orange with black patch. Legs black. Abdomen black. Posterior median eyes 0.8 diameter, lateral eyes 0.7 diameter of anterior medians. Anterior median eyes 0.6 diameter apart, posterior median eyes one diameter apart. Abdomen with pair of sclerotized shoulder tubercles and a median posterior hump (Fig. 437). Total length 9.0 mm. Carapace 3.6 mm long, 2.8 wide. First femur 3.4 mm; patella and tibia 3.9; metatarsus 2.4; tarsus 1.1. Second patella and tibia 3.1 mm; third 2.2; fourth 3.6.

Male. Coloration as in female except chelicerae, coxae all orange-yellow. Eyes slightly smaller than in female. Abdomen as in female (Fig. 438). Total length 6.5 mm. Carapace 3.1 mm long, 2.5 wide. First femur 3.1 mm; patella and tibia 3.6; metatarsus 2.1; tarsus 1.0. Second patella and tibia 2.7 mm; third 2.2; fourth 3.2.

Note. The male holotype is only 3.4 mm

total length, carapace 1.8 long, 1.6 wide; first patella and tibia, 2.1.

Variation. Females vary in total length from 7.7 to 9.0 mm, males from 3.4 to 6.5. A female and male from Quintana Roo (MCZ) are described and illustrated.

Diagnosis. Females are separated by the slightly sclerotized blunt shoulder tubercles, also present in the male (Figs. 437, 438). Unlike *A. septemmammata*, they have concave lips on the posterior margin of the epigynum, with the anterior and posterior margins of the lips parallel (Fig. 435). In posterior view, the lips are wider than those of *A. septemmammata* (Fig. 436). The male palpus differs by having a slight twist in the tegulum next to the median apophysis of the palpus (Fig. 439).

Natural History. The species is found in the forest in vertical webs, 50 cm to 1 m in diameter, which are built in small sink holes in the limestone. The spider rests in the hub and runs down the hub line when threatened (W. Maddison, personal communication).

Records. MEXICO *Quintana Roo*: Cobá [20°30′N; 87°44′W], 1 Feb. 1984, ♀, ♂ (V. B. Roth, MCZ); 31 km NE of Felipe, Carrillo Puerto [19°48′N; 87°52′W], 17 July 1983, ♀, 5 imm. (W. Maddison, R. S. Anderson, MCZ); 8 mi. NW of Tancan, Dos Bocas, 20 Nov. 1965, ♀ (J. G. Edwards, MCZ); Felipe Carrillo Puerto, 1 Aug. 1964, ♂ (J. C. Pallister, AMNH).

Alpaida urucuca new species
Figures 440–445; Map 4

Holotype. Female from Fazenda Antonio, Uruçuca, Bahia, Brazil, 24 Oct. 1979 (J. S. Santos, MCN no. 10972). The specific name is a noun in apposition after the locality.

Description. Female. Black patch containing two light spots on head; sides of the thorax yellow (Fig. 442). Chelicerae black distally. Sternum with four pairs of lateral white spots and median dark streak. Labium, endites, coxae light yellowish. Legs ringed black and light yellow. Dorsum of abdomen dusky yellowish with black pattern (Fig. 442), sides with white and black pigment, venter black with pair of white exclamation marks (Fig. 443). Abdomen pointed behind, no shoulder humps (Figs. 442). Total length 4.8 mm. Carapace 2.1 mm long, 1.5 wide. First femur 1.6 mm; patella and tibia 2.0; metatarsus 1.3; tarsus 0.7. Second patella and tibia 1.8 mm; third 1.2; fourth 1.9.

Male. Coloration as in female, except abdomen with more white pigment dorsally. Anterior median eyes 0.5 diameter apart, posterior median eyes 0.7 diameter apart. Total length 3.7 mm. Carapace 1.9 mm long, 1.7 wide. First femur 1.6 mm; patella and tibia 2.1; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.6 mm; third 1.2; fourth 1.8.

Diagnosis. Females are distinguished from those of *A. graphica* and *A. septemmammata* by the lack of shoulder humps and, in posterior view of the epigynum, wider lips ventrally (Fig. 441). Unlike those of the other two species, the males lack the basal prong of the median apophysis of the palpus (Fig. 445).

Paratype. BRAZIL *Bahia*: Fazenda Almada, Uruçuca, 27 Nov. 1977, ♂ (J. S. Santos, MCN 11159).

Alpaida championi (O. P.-Cambridge), new combination
Plate 2; Figures 446–451; Map 4

Epeira championi O. P.-Cambridge, 1889: 42, pl. 5, figs. 12, 13, ♀, ♂. Female, male syntypes from Bugaba, Panama (BMNH), lost.
Epeira aestimabilis Keyserling, 1892: 181, pl. 9, fig. 133, ♀. Female from Guatemala (BMNH), examined. NEW SYNONYMY.
Araneus championi:—F. P.-Cambridge, 1904: 517, pl. 50, figs. 1, 2, ♀, ♂. Bonnet, 1955: 457.
Aranea aestimabilis:—Roewer, 1942: 836.
Aranea championi:—Roewer, 1942: 839.
Araneus aestimabilis:—Bonnet, 1955: 425.

Note. The black underside of the abdomen and the projecting terminal apophysis of the male are illustrated by O. P.-Cambridge.

Description. Female from Costa Rica. Carapace yellowish. Labium, endites black. Sternum yellowish. Legs with black coxae,

yellowish femora, distal articles brown to black. Dorsum of abdomen with white longitudinal bands and white marks in middle (Fig. 448); venter black (Fig. 449). Abdomen elongate, oval. Total length 5.0 mm. Carapace 1.8 mm long, 1.5 mm wide. First femur 2.4 mm; patella and tibia 2.7; metatarsus 1.8; tarsus 0.8. Second patella and tibia 2.3 mm; third 1.5; fourth 2.3.

Male. Coloration as in female (Fig. 450). Shape of abdomen as in female. Total length 3.4 mm. Carapace 1.8 mm long, 1.5 mm wide. First femur 2.1 mm; patella and tibia 2.4; metatarsus 1.5; tarsus 0.7. Second patella and tibia 1.8 mm; third 1.2.

Variation. Females vary in total length from 3.6 to 5.0 mm, males from 3.1 to 3.5. The female and male described and illustrated came from Costa Rica.

Diagnosis. Females are distinguished from those of *A. xavantina* by the abdominal markings (Figs. 448, 449) and from *A. tuonabo* by the small lobe and anterior notch of the epigynum (Fig. 446). The males are distinguished from *A. xavantina* and *A. tuonabo* by the round, lobed median apophysis (Fig. 451).

Natural History and Distribution. The species is found in lowland forest near water in Costa Rica. The web is illustrated (Plate 2). It is found from Guatemala to southern Colombia and is most common in Costa Rica (Map 4).

Records. COSTA RICA *Heredia*: La Selva nr. Puerto Viejo, Jan. 1978, ♀, June 1982, ♂, ♀, 14 Jan. 1984, ♀ (W. Eberhard, MCZ). *Cartago*: Turrialba, May 1944, 2♀ (F. Schrader, AMNH). *San José*: San Isidro del General, 2♀, 3♂ (D. Rounds, MCZ). *Puntarenas*: Reserva Biologica Carara nr. Tárcoles, 28 July 1983, 3♀ (H. W. Levi, W. Eberhard, MCZ), Aug. 1983, ♀ (W. Eberhard, MCZ); 6 km S San Vito, 08°42′N, 83°00′W, Mar. 1967, ♀ (OTS, MCZ); Parque Nac. Corcovado, Horona, 20 Aug. 1978, ♂, ♀ (Y. D. Lubin, MCZ); Osa Peninsula, 2.5 mi SW Rincon, 1967, ♀ (OTS, MCZ); Osa Peninsula, Sirena, Feb. 1984, ♀ (W. Eberhard, MCZ). COLOMBIA *Nariño*: La Planada, 1,800 m, 7 km S Choconés, nr. Ricaurte, July 1986, ♀ (W. Eberhard, MCZ).

Alpaida xavantina new species
Figures 452–457; Map 4

Holotype. Male holotype and female paratype from 12°49′S, 51°46′W, 260 km N of Xavantina, 400 m, cerrado shrub, Est. Mato Grosso, Brazil, Feb.–Apr. 1969, (Xavantino-Cachimbo Expedition, ex MCZ, MZSP). The specific name is a noun in apposition after the locality.

Description. Female. Carapace light yellowish with white pigment spot in center of thorax. Labium, sternum, endites black. Coxae and legs yellowish. Abdomen with white pigment patches on dorsum (Fig. 454), sides with a wide white band; venter black with two parallel white pigment lines, white behind spinnerets (Fig. 455). Abdomen oval, pointed behind (Fig. 454). Total length 4.0 mm. Carapace 1.4 mm long, 1.1 wide. First femur 1.6 mm; patella and tibia 1.7; metatarsus 1.1; tarsus 0.5. Second patella and tibia 1.4 mm; third 0.9; fourth 1.2.

Male. Coloration as in female (Fig. 456). Second tibia not swollen, without macrosetae. Total length 3.4 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.6 mm; patella and tibia 1.8; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.4 mm; third 0.8; fourth 1.3.

Variation. Males vary from 3.0 to 3.4 mm. The male holotype and a female collected with it are described and illustrated.

Diagnosis. Females differ from those of *A. championi* by the oval shape of the abdomen (Fig. 454) and by the larger median plate in posterior view (Fig. 453). The male differs from those of *A. championi* by the oval median apophysis (Fig. 457) and from this and other *Alpaida* by the S-curved embolus and the sculpturing of the terminal apophysis (Fig. 457).

Natural History. Specimens have been found in cerrado shrub in Mato Grosso.

Paratypes. BRAZIL *Pará*: Belém, Aug. 1971, ♂ (M. E. Galiano, MACN 8418). *Mato Grosso*: 260 km N of Xavantina, Feb.–Apr. 1969, ♂ (Xavantino-Cachimbo Exp., MCZ).

Alpaida tayos new species
Figures 458–467; Map 4

Holotype. Female from Los Tayos-Santiago, banana plantation, 3°04'S, 78°02'W Prov. Morona-Santiago, Ecuador, 3 Aug. 1976 (MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, yellowish, rims of thorax dusky. Labium, endites, sternum, black. Coxae, legs, dusky yellowish. Dorsum of abdomen white, posterior tip black (Figs. 462, 463); sides dusky; venter black (Fig. 465). Abdomen oval, pointed behind (Figs. 462, 463). Total length 3.7 mm. Carapace 1.5 mm long, 1.0 wide. First femur 1.7 mm; patella and tibia 1.8; metatarsus 1.2; tarsus 0.7. Second patella and tibia 1.5 mm; third 0.9; fourth 1.3.

Male. Coloration as in female, except dorsum of abdomen darker on sides (Fig. 466). Lateral eyes 0.8 diameter of median eyes. Anterior median eyes slightly less than their diameter apart; posterior medians their diameter apart. Second tibiae not thicker than first. Total length 3.1 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.6 mm; patella and tibia 1.8; metatarsus 1.1; tarsus 0.5. Second patella and tibia 1.4 mm; third 0.9; fourth 1.3.

Variation. Total length of females from 3.1 to 4.5 mm, males from 2.7 to 3.4 mm. The distance of the median notch of the epigynum from its posterior margin seems variable.

The female holotype is described and illustrated (Figs. 458, 459, 462, 465) and a male from Dpto. Huánuco, Peru (AMNH).

Diagnosis. Females differ from those of *A. championi* by the oval shape and coloration of the abdomen (Figs. 462–464) and from those of both *A. championi* and *A. xavantina* by the straighter posterior edge of the epigynum (Fig. 458) and its oval posterior median plate (Fig. 459). The males differ from those of *A. xavantina* by having a much thicker basal prong on the terminal apophysis and by the larger conductor (Fig. 467).

Natural History and Distribution. A female has been collected from a banana plantation. The species is found from Ecuador to Pará state, Brazil (Map 4).

Paratypes. GUYANA *Bartica Distr.*: Kartabo 1922, 1924, 2♀ (AMNH). ECUADOR *Napo*: headwaters of Río Arajuno, 1,000 m, 28 Apr. 1938, ♀ (W. Clarke-Macintyre, AMNH). PERU *Huánuco*: Tingo María, 8 Oct. 1946, ♀; 21 Nov. 1946, ♂; 19–25 May 1947, ♂, ♀ (J. C. Pallister, AMNH, MCZ). *Madre de Dios*: Puerto Maldonado, 100 m, 16–23 Apr. 1947, ♂ (J. C. Pallister, AMNH). BRAZIL *Pará*: Marituba, Ananindeua, Nov. 1963, ♀ (M. Oliveira, P. Wygodzinsky, AMNH); Canindé, Rio Gurupi, Apr. 1963, ♀ (B. Malkin, AMNH).

Alpaida nancho new species
Figures 468–471; Map 4

Holotype. Female from Montaña de Nancho, 3,000 m, Dpto. Cajamarca, Peru (K. Jelski, J. Sztolcman, PAN). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum orange. Legs orange, distal ends of articles with thin black rings. Dorsum of abdomen with median white band bordered by small paired black patches (Fig. 470); venter with black rectangular patch framed by white (Fig. 471). Carapace with slight white pubescence. Abdomen pointed behind, with small anterior median

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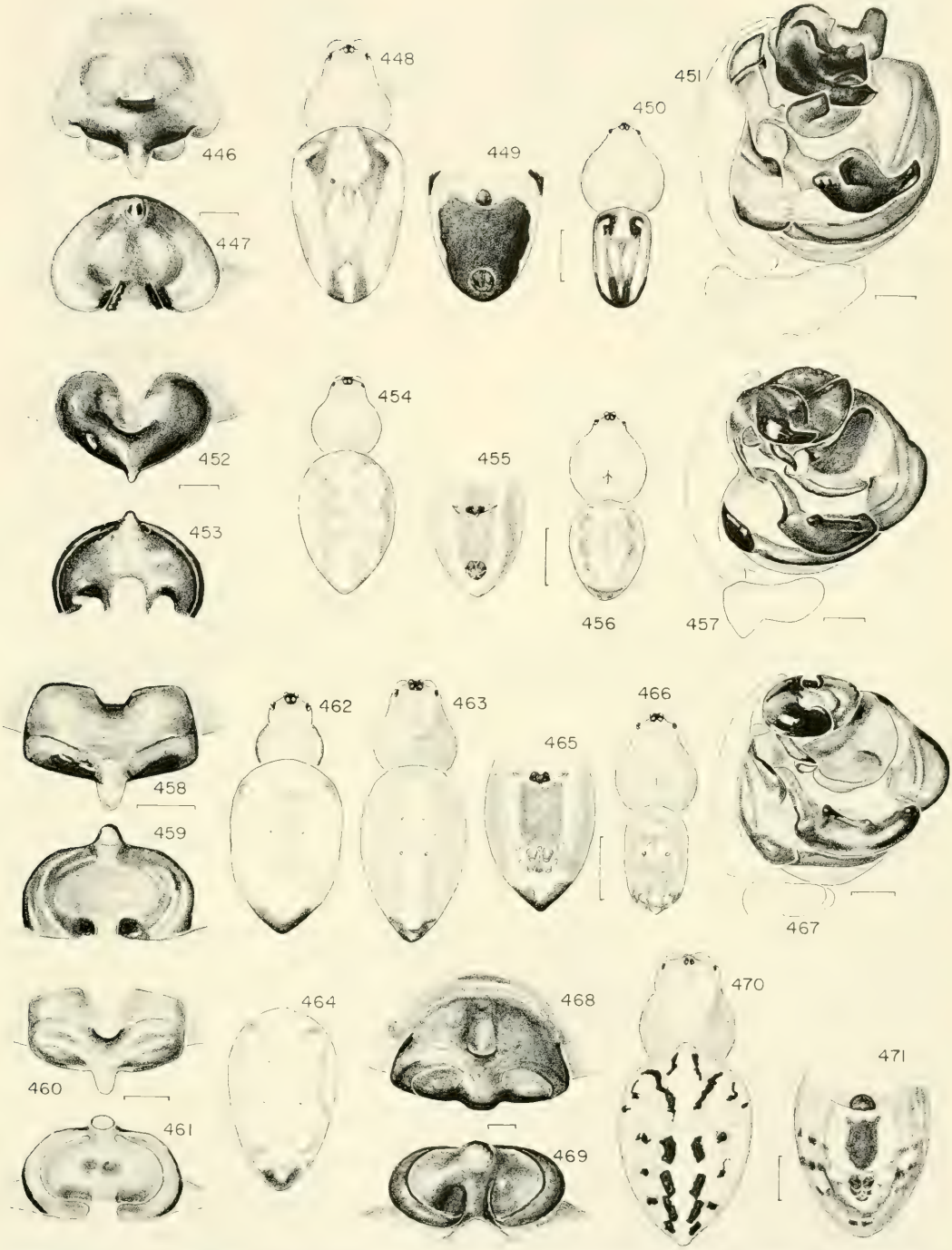
Figures 468–471. *A. nancho* n. sp., female. 468, epigynum, ventral. 469, epigynum, posterior. 470, dorsal. 471, ventral. *Scale lines*. 1.0 mm; genitalia, 0.1 mm.

Figures 446–451. *Alpaida championi* (O. P.-Cambridge). 446–449, female. 446, epigynum, ventral. 447, epigynum, posterior. 448, dorsal. 449, ventral. 450, 451, male. 450, dorsal. 451, left palpus.



Figures 452–457. *A. xavantina* n. sp. 452–455, female. 452, epigynum, ventral. 453, epigynum, posterior. 454, dorsal. 455, ventral. 456, 457, male. 456, dorsal. 457, palpus.

Figures 458–467. *A. tayos* n. sp. 458–465, female. 458, 460, epigynum, ventral. 459, 461, epigynum, posterior. 458, 459, (Ecuador). 460, 461, (Peru). 462–464, dorsal. 465, ventral. 466, 467, male. 466, dorsal. 467, palpus.

hump (Fig. 470). Total length 6.5 mm. Carapace 2.4 mm long, 2.0 wide. First femur 1.9 mm; patella and tibia 2.3; metatarsus 1.3; tarsus 0.6. Second patella and tibia 2.0 mm; third 1.4; fourth 2.0.

Diagnosis. The concavely curved lips of the epigynum, which expose the posterior median plates on each side in ventral view, and the anterior position of the notch, are diagnostic (Fig. 468).

Alpaida delicata (Keyserling), new combination
Figures 472–478; Map 5

Epeira delicata Keyserling, 1892: 183, pl. 9, fig. 135, ♀, ♂. Six female, four male syntypes from Espírito Santo, Brazil (BMNH), examined.

Araneus taczanowskii Simon, 1897b: 473. Female holotype from Tefé, Est. Amazonas, Brazil (MNHN), examined. Bonnet, 1955: 609. NEW SYNONYMY.

Aranea delicata:—Roewer, 1942: 840.

Aranea taczanowski:—Roewer, 1942: 853.

Araneus delicatus:—Bonnet, 1955: 485.

Description. Female. Carapace light orange, darker in center. Sternum, legs light orange. Dorsum of abdomen with white and black marks (Fig. 474); venter without pigment. Carapace with few setae in center of thorax. Abdomen with a median anterior hump and a pair of posterior humps (Fig. 474). Total length 5.0 mm. Carapace 2.1 mm long, 1.5 wide. First femur 2.3 mm; patella and tibia 2.8; metatarsus 2.1; tarsus 0.9. Second patella and tibia 2.5 mm; third 1.5; fourth 2.4.

Male. Coloration as in female (Fig. 476). Posterior median eyes, lateral eyes each 0.8 diameter of anterior median eyes. Anterior median eyes half their diameter apart, posterior median eyes 0.6 their diameter apart. Second tibiae widest at tibial tarsal joint, with strong pairs of macrosetae. First tibiae also with pair of macrosetae on distal end (Fig. 478). Abdomen as in female (Fig. 476). Total length 5.4 mm. Carapace 2.4 mm long, 1.9 wide. First femur 3.3 mm; patella and tibia 4.1; metatarsus 3.2; tarsus 1.1. Second patella and tibia 3.3 mm; third 2.1; fourth 3.2.

Note. Cymbium lacks tarsal organ always present in metids. One male lacks palpal tarsi on both palpi as do some *Herennia* males in Papua New Guinea, which defend their mated females from other males.

Variation. Total length of females from 4.7 to 6.0 mm, males 3.9 to 5.4. The length of the palpal tibia varies from just longer than wide to longer than the tarsal cymbium (Fig. 477).

A female from Tefé (MCZ) and a male from Mato Grosso (AMNH) are described and illustrated.

Diagnosis. The female is distinguished from all *Alpaida* except *A. truncata* by two black humps on the truncate posterior end of the abdomen (Fig. 474); it differs from *A. truncata* by its smaller size and the shape of the epigynum, which has a curved posterior margin and a small median knob (Fig. 472). The male differs from all other *Alpaida* males by having the palpal tibia as long as wide to longer than the cymbium (Fig. 477).

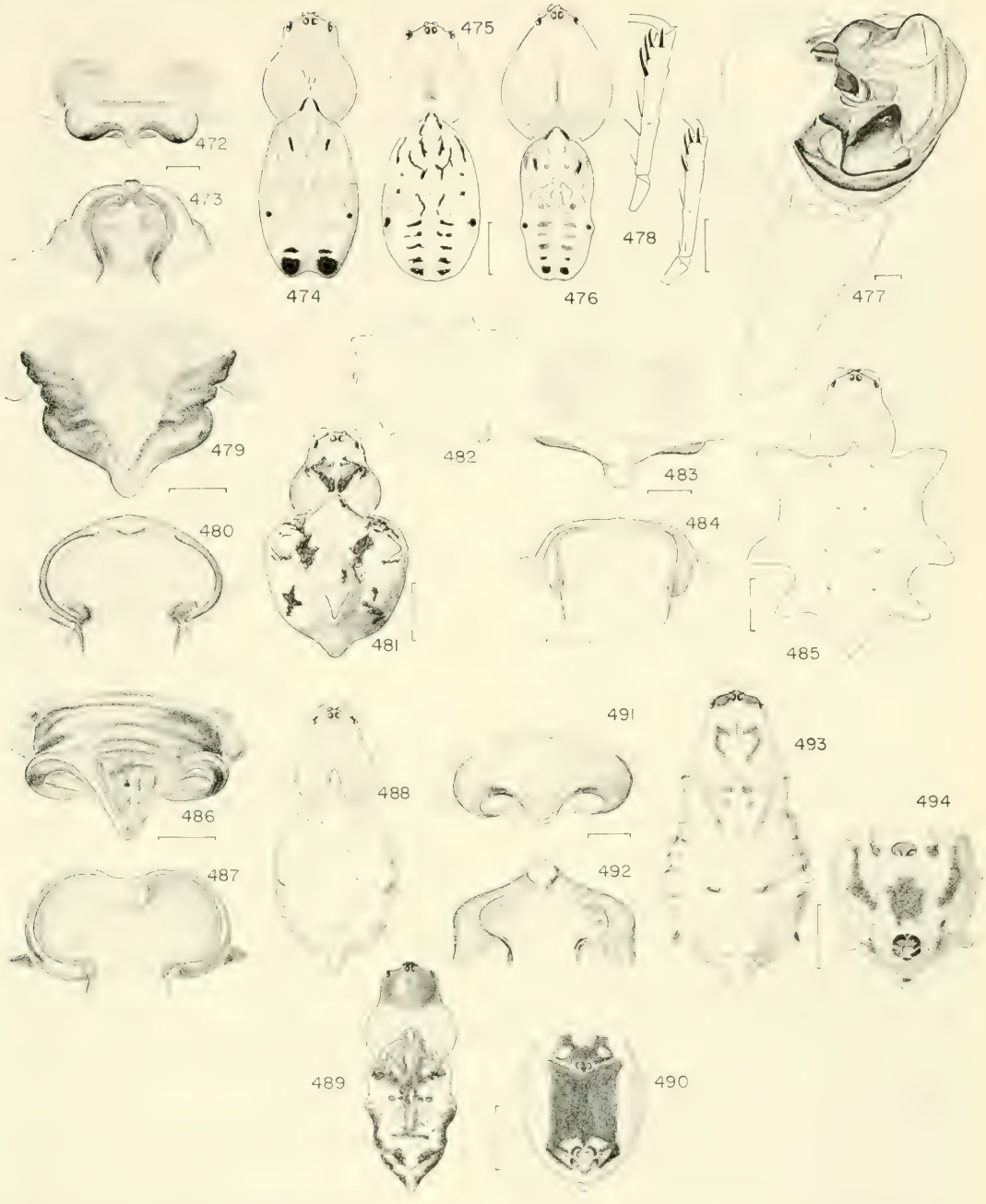
Records. PERU *Ucayali*: Colonia Calleria, Río Calleria, 15 km from Ucayali, Sept., Oct. 1961, ♂, ♀ (B. Malkin, AMNH). BRAZIL *Amazonas*: Tefé, Nov., Dec. 1919, 5♀, ♂ (H. S. Parrish, MCZ). *Pará*: Jacazeacanga, Oct. 1959, ♂ (M. Alvarenga, AMNH). *Mato Grosso*: [no locality] Oct. 1976, 2♀, 3♂ (M. Alvarenga, AMNH). BOLIVIA [?] General Roman, Feb. 1952, ♀ (Martinez, MLP).

Alpaida atomaria (Simon), new combination
Figures 479–482; Map 5

Salassina atomaria Simon, 1895: 781. Two female syntypes from Tijuca, Rio de Janeiro, Brazil (MNHN no. 8515), examined.

Edricus atomarius:—Roewer, 1942: 761. Bonnet, 1956: 1648.

Description. Female. Carapace brown, two black patches in thoracic region (Fig. 481). Legs yellow-brown with faint rings on venter. Dorsum of abdomen with paired black spots and numerous small white pigment spots (Fig. 481); venter without pigment in center; a black patch on each side;



Figures 472–478. *Alpaida delicata* (Keyserling). 472–475, female. 472, epigynum, ventral. 473, epigynum, posterior. 474, 475, dorsal. 476–478, male. 476, dorsal. 477, left palpus. 478, left first and second tibiae, ventral.

Figures 479–482. *A. atomaria* (Simon), female. 479, epigynum, ventral. 480, epigynum, posterior. 481, dorsal. 482, lateral.

Figures 483–485. *A. octolobata* n. sp., female. 483, epigynum, ventral. 484, epigynum, posterior. 485, dorsal.

Figures 486–490. *A. ericae* n. sp., female. 486, epigynum, ventral. 487, epigynum, posterior. 488, 489, dorsal. 490, ventral.

Figures 491–494. *A. yucuma* n. sp., female. 491, epigynum, ventral. 492, epigynum, posterior. 493, dorsal. 494, ventral.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

spinnerets dark brown. Anterior median eyes are 1.5 diameters apart, posterior medians 1.2 diameters apart. Abdomen with one anterior median and two posterior median humps, and a pair of lateral humps (Figs. 481, 482). Total length 4.0 mm. Carapace 1.6 mm long, 1.3 wide. First femur 1.7 mm; patella and tibia 1.8; metatarsus 1.1; tarsus 0.6. Second patella and tibia 1.6 mm; third 0.8; fourth 1.6.

Variation. Total length of the females available varies from 2.9 to 4.9 mm.

Diagnosis. The female is distinguished by the markings on the thorax and the humps on the abdomen (Figs. 481, 482), and by the epigynum, which has a median lobe whose margins continue posteriorly into the posterior margin of the lips, and the dark sides and spherical seminal receptacles visible anteriorly (Fig. 479).

Record. BRAZIL *Rio de Janeiro*: Represa Rio Grande, [22°55′S, 43°25′W] Feb. 1976, ♀ (M. Alvarenga, AMNH).

Alpaida octolobata new species
Figures 483–485; Map 5

Holotype. Female holotype and one female and one immature paratype from Montenegro, Rio Grande do Sul, Brazil, 15 Dec. 1977 (A. A. Lise, MCN no. 07513). The specific name is a descriptive adjective.

Description. Female. Carapace, sternum and legs yellowish white. Dorsum of abdomen with small white pigment spots, densest on venter around sides. Abdomen with three pairs of lobes, and an anterior and posterior median lobe (Fig. 485). Total length 5.7 mm. Carapace 2.1 mm long, 1.7 wide. First femur 3.1 mm; patella and tibia 3.1; metatarsus 2.1; tarsus 0.8. Second patella and tibia 2.7 mm; third 1.7; fourth 2.5.

Diagnosis. The weakly sclerotized epigynum with dark posterior edge and small lobe in ventral view (Fig. 483); in posterior view the lip widens dorsally on each side (Fig. 484).

Paratype. BRAZIL *Bahia*: Fazenda Nossa Senhora das Neves, Itamaraju, 7 Aug. 1978, ♀ (J. S. Santos, MCN 11074).

Alpaida ericae new species
Figures 486–490; Map 5

Holotype. Female from Montenegro, Rio Grande do Sul, Brazil, 17 Oct. 1977 (E. H. Buckup, MCN no. 7268). The species is named after the collector.

Description. Female. Carapace light orange-yellow. Labium, sternum, endites, black. Coxae orange-yellow; legs light orange-yellow with patches on venter. Dorsum of abdomen with white pigment and dusky markings (Figs. 488, 489); sides white; venter black (Fig. 490). Anterior median eyes more than one; posterior median eyes more than 1.5 diameters apart. First femora with two prolateral macrosetae. Abdomen with four pairs of lateral humps, one anterior and two median posterior (Figs. 488, 489). Total length 4.2 mm. Carapace 1.5 mm long, 1.2 wide. First femur 1.5 mm; patella and tibia 1.8; metatarsus 1.0; tarsus 0.5. Second patella and tibia 1.5 mm; third 1.0; fourth 1.4.

Variation. Total length of females varies from 3.7 to 4.7 mm. Some females have black heads; some have less distinct humps than the one illustrated (Figs. 488, 489).

Diagnosis. Unlike other *Alpaida*, the median lobe of the epigynum is large, wider than each side lobe (Fig. 486).

Paratypes. BRAZIL *Rio Grande do Sul*: Montenegro, 6 Oct. 1977, ♀ (A. A. Lise, MCN), 3 Nov. 1977, ♀ (E. H. Buckup, MCN 7149); Passo do Inferno, São Francisco de Paula, 20 Apr. 1979, ♀ (A. A. Lise, MCN 8554). ARGENTINA *Buenos Aires*: Isla Martín García, Río de la Plata, 2 Dec. 1965, ♀ (M. E. Galiano, MEG).

Alpaida yucuma new species
Figures 491–494; Map 5

Holotype. Female from Salto do Yucumã, Parque Estadual do Turvo, Tenente Portela, Rio Grande do Sul, Brazil (A. A. Lise, MCN no. 12855). The specific name is a noun in apposition after the locality.

Description. Female. Carapace off-white with black marks (Fig. 493) and a black patch on each side between median and lateral eyes. Sternum off-white. Legs

off-white with longitudinal indistinct dusky marks. Dorsum of abdomen white with indistinct dusky marks (Fig. 493); venter with black patch in middle, black patches on sides; spinnerets black (Fig. 494). Abdomen slightly longer than wide with four pairs of lateral humps, the second small, a small anterior median hump and a larger median posterior (Fig. 493). Total length 4.7 mm. Carapace 1.7 mm long, 1.3 wide. First femur 1.5 mm; patella and tibia 1.7; metatarsus 0.9; tarsus 0.5. Second patella and tibia 1.4 mm; third 0.9; fourth 1.5.

Diagnosis. Female is distinguished by the black marks between median and lateral eyes and the small rounded lobe between concave posterior margins of the epigynum (Fig. 491).

Alpaida rosa new species
Figures 495–500; Map 5

Holotype. Female holotype and one female paratype from Santa Rosa, Rio Grande do Sul, Brazil, 2 Jan. 1984 (A. D. Brescovit, MCN no. 11916). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellowish with a black patch on each side of head (Fig. 497). Labium, sternum black. Endites with black patch. Legs yellowish. Dorsum of abdomen white with paired black spots (Fig. 497); venter black with white on each side (Fig. 498). Anterior median eyes their diameter apart; posterior median eyes 0.7 diameter apart. Abdomen pointed behind. Total length 4.2 mm; carapace 1.7 mm long, 1.3 wide. First femur 1.5 mm; patella and tibia 1.7; metatarsus 1.1; tarsus 0.5. Second patella and tibia 1.5 mm; third 1.1; fourth 1.6.

Male. Coloration as in female. Anterior median eyes 0.6 their diameter apart; posterior median eyes 0.7 their diameter apart. Second tibiae with macrosetae. Total length 3.1 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.5 mm; patella and tibia 1.8; metatarsus 1.1; tarsus 0.5. Second patella and tibia 1.3 mm; third 0.9; fourth 1.6.

Variation. Females vary in total length from 4.2 to 5.6 mm. The female holotype and a male from Salta Prov., Argentina are described and illustrated.

Diagnosis. The females are distinguished from all other *Alpaida* by the parallel sides of the lobe of the epigynum and, in ventral view of the posterior median plate, by two sets of lips, one inside the other's convex curve (Fig. 495). In posterior view there are also two lips, an outer one, and an inner one that coils posteriorly (Fig. 496). The male is distinguished by the wide basal prong and the two distal tips of the terminal apophysis (Fig. 500).

Paratypes. BRAZIL *Rio Grande do Sul*: Salto do Jacui, Espumoso, 14 Jan. 1982, ♀ (A. A. Lise, MCN 9987). ARGENTINA *Misiones*: Parque Nac. Iguazu, Jan. 1966, ♀ (M. E. Galiano, MACN 8420); Eldorado, 1964, ♀ (A. Kovacs, AMNH). *Salta*: Orán, 8 Dec. 1950, 2♀ ♂ (M. Biraben, MLP).

Alpaida calotypa (Chamberlin), new combination
Figures 501–505; Map 5

Epeira nigropunctata Taczanowski, 1878: 167, pl. 2, fig. 17, ♀. Female lectotype here designated and five juvenile paralectotypes from Paltaypampa [1,860 m, Junín, prov. Tarma], female paralectotype from Uaca Pistana [?], one male, two female paralectotypes from Pumamarca [1,900 m, Junín, prov. Tarma], Peru (PAN), examined. (Name preoccupied by *E. nigropunctata* L. Koch, 1871.)

Aranea calotypa Chamberlin, 1916: 256, pl. 19, fig. 4, ♂. Male holotype from Lucma, 7,000 ft. [2,000 m, Dpto. Cuzco], Peru (MCZ), examined. Roewer, 1942: 838, NEW SYNONYMY.

Aranea nigropunctatula Roewer, 1942: 848. New name since *Epeira nigropunctata* is preoccupied by L. Koch, 1871.

Araneus calotypus:—Bonnet, 1955: 450.

Araneus nigropunctatus:—Bonnet, 1955: 550.

Note. The description of Taczanowski is based on several specimens from different localities and is a mixture of species. Each locality vial had a different species. The choosing of the lectotype was in part arbitrary, in part it matched Taczanowski's illustration. Also the lectotype comes from the first locality mentioned by Taczanowski.

Description. Female. Carapace, sternum, legs yellow-white. Dorsum of abdomen white with two black spots at posterior end (Fig. 503) and about two tiny black spots on humps on each side, two anterior, two posterior; venter with scattered white pigment spots. Anterior median eyes one diameter apart, posterior medians 1.5 diameters apart. Abdomen longer than wide with anterior median hump and slight humps on each side each bearing a black spot, sides with indistinct grooves (Fig. 503). Total length 5.5 mm. Carapace 2.6 mm long, 2.0 wide. First femur 2.2 mm; patella and tibia 2.6; metatarsus 1.6; tarsus 0.7. Second patella and tibia 2.2 mm; third 1.4; fourth 2.2.

Male. Coloration as in female (Fig. 504). Anterior median eyes largest, posterior medians 0.8 diameter of anterior medians, laterals both about 0.7 diameter of anterior medians. Anterior medians their diameter apart, posterior medians 1.3 their diameters apart. Second tibiae swollen and with macrosetae. Abdomen oval. Total length 4.5 mm. Carapace 2.4 mm long, 2.1 wide. First femur 2.2 mm; patella and tibia 2.7; metatarsus 1.5; tarsus 0.7. Second patella and tibia 1.6 mm; third 1.4; fourth 2.0.

Variation. Total length of females varies from 5.5 to 8.5 mm, males from 4.5 to 5.7. Females from Tingo María have the scape of the epigynum broken off and have a wider abdomen with shoulder humps and a lateral dark line. They may belong to a different species. Females from Ollanta, Cuzco, also have the tips broken off and are the largest specimens; they also have a dusky line through the median of the carapace.

The female lectotype and a male paralectotype are described and illustrated.

Diagnosis. In ventral view the epigynum has a long scape containing a deep notch; the bulge of the posterior median plate shows on each side (Fig. 501). Males are distinguished by having two equal-sized, curved hooks on the terminal apophysis and a blunt curved lobe on the median apophysis (Fig. 505).

Records. PERU *Huánuco*: Tingo María, 25 May 1947, ♀, imm. (J. C. Pallister, AMNH). *Cuzco*: Ollanta, 6 June 1961, 2♀ (N. L. H. Kraus, AMNH); Río Tinccochaca, Aug. 1911, ♂ paratype of *calotypa* (Yale Peruvian Exped., MCZ); below Lucma, 2,000 m, 25 Aug. 1911, ♂ (Yale Peruvian Exped., MCZ). [?] Palatayoc, ♂, ♀ (K. Jelski, J. Stolcman, PAN).

Alpaida conica O. P.-Cambridge
Figures 506–511; Map 5

Alpaida conica O. P.-Cambridge, 1889: 53, pl. 4, fig. 3, ♀. Female holotype from Bugaba, Panama, (BMNH) examined. Keyserling, 1893: 281, pl. 14, fig. 207, ♀. Bonnet, 1955: 267.

Aranea conica:—F. P.-Cambridge, 1904: 519.

Aranea coniformis:—Roewer, 1942: 839. New name for *A. conica* (thought preoccupied by *Aranea conica* Pallas).

Description. Female. Carapace orange yellow with black patch on each side (Fig. 508). Labium, sternum black; endites, yellow. Legs dusky yellow. Dorsum of abdomen with median white longitudinal line bordered by paired lateral black and dusky patches (Fig. 508); sides dorsally a white

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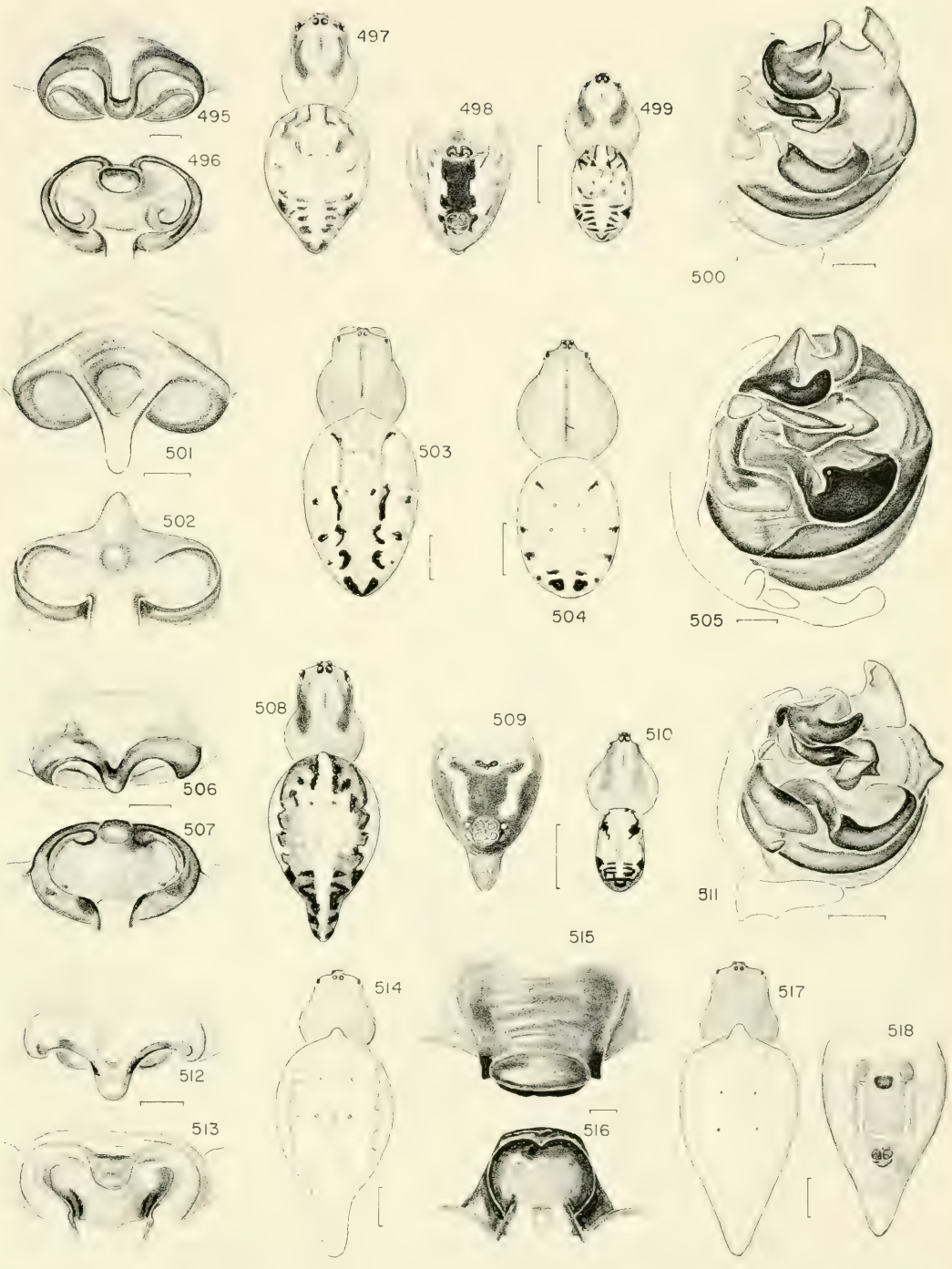
Figures 495–500. *Alpaida rosa* n. sp. 495–498, female. 495, epigynum, ventral. 496, epigynum, posterior. 497, dorsal. 498, ventral. 499, 500, male. 499, dorsal. 500, left palpus.

Figures 501–505. *A. calotypa* (Chamberlin). 501–503, female. 501, epigynum, ventral. 502, epigynum, posterior. 503, dorsal. 504, 505, male. 504, dorsal. 505, palpus.

Figures 506–511. *A. conica* O. P.-Cambridge. 506–509, female. 506, epigynum, ventral. 507, epigynum, posterior. 508, dorsal. 509, ventral. 510, 511, male. 510, dorsal. 511, palpus.

Figures 512–514. *A. gracia* n. sp., female. 512, epigynum, ventral. 513, epigynum, posterior. 514, dorsal.



Figures 515–518. *A. costai* n. sp., female. 515, epigynum, ventral. 516, epigynum, posterior. 517, dorsal. 518, ventral. *Scale lines*. 1.0 mm; genitalia, 0.1 mm.

longitudinal band, posterior to it a round black patch, ventrally a dusky band; venter black with white line on each side (Fig. 509) dusky behind spinnerets. Chelicerae with three anterior and three posterior teeth. Abdomen oval with narrow posterior cone (Fig. 508). Total length 4.4 mm. Carapace 1.6 mm long, 1.2 wide. First femur 1.4 mm; patella and tibia 1.7; metatarsus 0.9; tarsus 0.5. Second patella and tibia 1.5 mm; third 0.9; fourth 1.5.

Male. Coloration as in female. Abdomen oval with posterior median hump (Fig. 510). Total length 2.4 mm. Carapace 1.3 mm long, 1.1 wide. First femur 1.2 mm; patella and tibia 1.5; metatarsus 0.8; tarsus 0.5. Second patella and tibia 1.2 mm; third 0.8; fourth 1.1.

Variation. Total length of males varies from 2.4 to 2.9 mm.

A female and male (MCZ) are described and illustrated.

Diagnosis. The female differs from sympatric species of *Alpaida* by the shape of the abdomen, the lack of shoulder humps and a tail posterior to spinnerets (Fig. 508). The male differs by a thorn on the corner of the median apophysis closest to the radix and by the curved basal hook and distal extension of the terminal apophysis (Fig. 511).

Records. PANAMA *Panamá*: Summit Park, 27 Dec. 1957, ♂ (A. M. Chickering, MCZ); Forest Preserve, 25 July 1954, ♀ (A. M. Chickering, MCZ); Balboa, 17 Aug. 1936, ♂ (A. M. Chickering, MCZ).

Alpaida gracia new species
Figures 512–514; Map 5

Holotype. Female from Alta Gracia, Prov. Córdoba, Argentina, Feb. 1934 (C. Bruch, MACN no. 8489). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, legs, orange-yellow. Dorsum of abdomen white with two longitudinal bands of denser white pigment (Fig. 514); venter white. Abdomen elongate with anterior median hump and long tail (which is damaged in holotype specimen); length of abdomen posterior to spinnerets more than twice the distance from spinnerets to epigynum. Total length 6.5 mm. Carapace 2.1 mm long, 1.6 wide. First femur 1.5 mm; patella and tibia 1.8; metatarsus 1.1; tarsus 0.5. Second patella and tibia 1.7 mm; third 1.1; fourth 1.7.

Diagnosis. This female is similar to *A. conica* but differs by having the lobe of the epigynum projecting more posteriorly and the lips on each side less posteriorly (Fig. 512).

Alpaida costai new species
Figures 515–518; Map 5

Holotype. Female holotype and four female paratypes from José C. Paz, Prov. Buenos Aires, Argentina (Rosas Costa, MLP). The species is named after the collector.

Description. Female. Carapace, sternum, legs orange. Dorsum of abdomen whitish; venter with two parallel longitudinal white lines enclosing a dusky area (Fig. 518). Eyes small. Anterior median eyes 1.7 times their diameter apart; posterior median eyes twice their diameter apart. Abdomen with anterior median hump and a tail (Fig. 517). Total length 7.8 mm. Carapace 2.5 mm long, 1.9 wide. First femur 1.7 mm; patella and tibia 2.3; metatarsus 1.3; tarsus 0.7. Second patella and tibia 2.0 mm; third 1.3; fourth 1.9.

Note. All type specimens are in poor physical condition, having once been dry.

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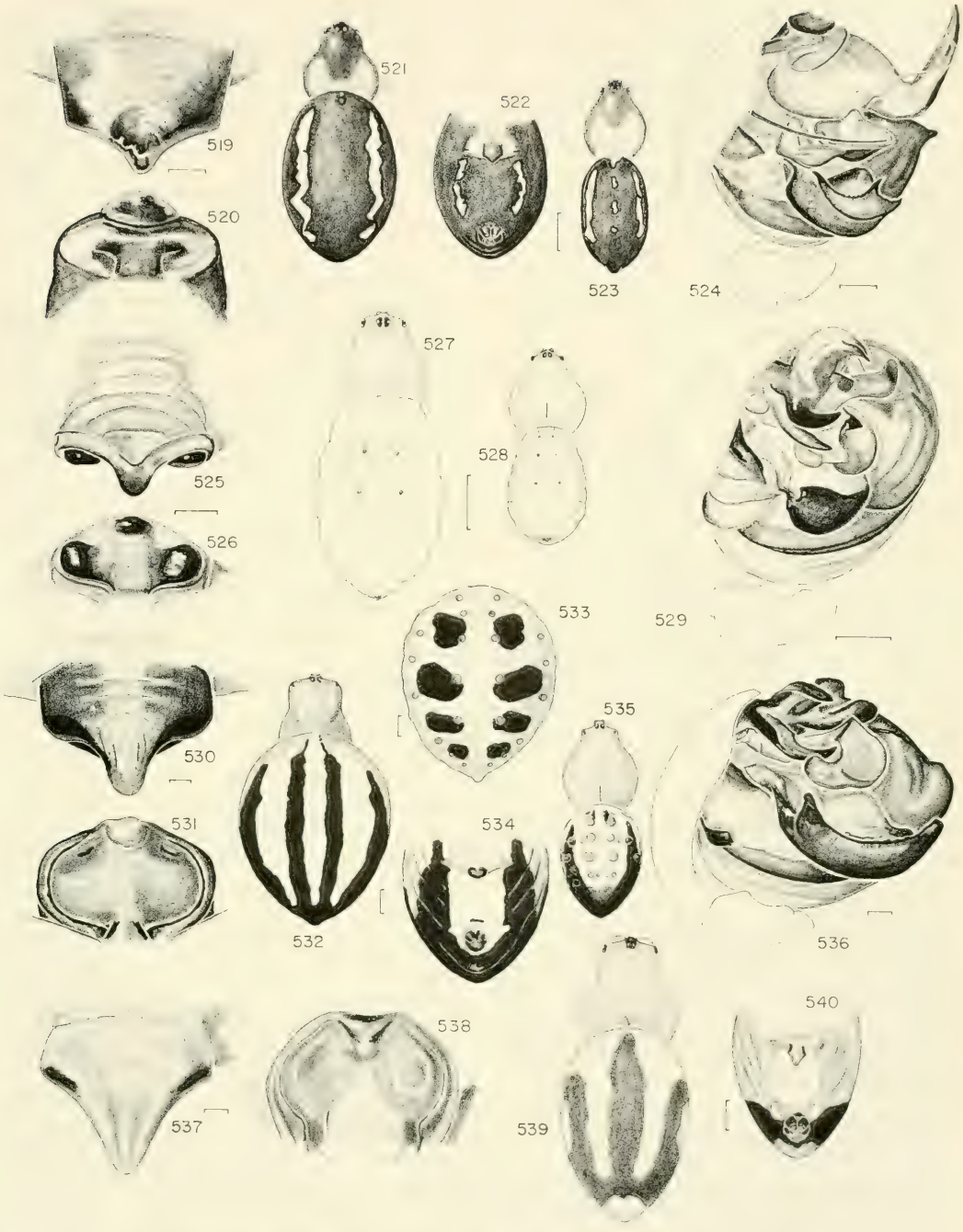
Figures 519–522. *Alpaida muco* n. sp., female. 519, epigynum, ventral. 520, epigynum, posterior. 521, dorsal. 522, ventral.

Figures 523, 524. *A. utiariti* n. sp. male. 523, dorsal. 524, left palpus.

Figures 525–529. *A. albocincta* (Mello-Leitão). 525–527, female. 525, epigynum, ventral. 526, epigynum, posterior. 527, dorsal. 528, 529, male. 528, dorsal. 529, palpus.



Figures 530–537. *A. quadrilorata* (Simon). 530–534, female. 530, epigynum, ventral. 531, epigynum, posterior. 532, 533, dorsal. 534, ventral. 535, 536, male 535, dorsal. 536, palpus.

Figures 537–540. *A. angra* n. sp., female. 537, epigynum, ventral. 538, epigynum, posterior. 539, dorsal. 540, ventral.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

The transverse posterior piece of the epigynum (Fig. 515) is torn off in all specimens but the holotype.

Diagnosis. This species differs from other *Alpaida* by the elongate abdomen with an anterior median hump (Fig. 517), by the epigynum, which is a ventrally projecting bulge with a sclerotized tip on each side (Fig. 515), and, in posterior view, by the heart-shaped convex median plate (Fig. 516). (It is not certain if the specimen has the lobe of the epigynum torn off or if it never had a median lobe.)

Alpaida muco new species
Figures 519–522; Map 5

Holotype: Female from 20 km N of Río Muco, 175 m, Dpto. Meta, Colombia, 1978 (W. E. Eberhard no. 1348, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace black, sides of thorax orange, rims black. Sternum, orange. Coxae, distal leg articles black. Dorsum of abdomen, black with a pair of white longitudinal lines (Fig. 521); venter black with a pair of white lines (Fig. 522). Fourth legs longer than first. Abdomen oval. Total length 4.2 mm. Carapace 1.7 mm long, 1.3 wide. First femur 1.5 mm; patella and tibia 1.8; metatarsus 1.1; tarsus 0.7. Second patella and tibia 1.5 mm; third 1.1; fourth 1.8.

Note. The male of this species may be *A. utiariti.*

Diagnosis. The dark color, oval abdomen (Fig. 521), pentagonal shape of the epigynum in ventral view (Fig. 519) and two curved grooves in the median plate in posterior view (Fig. 520) separate the female from other species.

Alpaida utiariti new species
Figures 523, 524; Map 5

Holotype. Male from Utiaritĺ, Mato Grosso, Brazil, July 30, 1961 (K. Lenko, MZSP no. 3572). The specific name is a noun in apposition after the locality.

Description. Male. Head and edge of thorax black, thorax orange. Labium, endites black. Sternum orange with some white pigment. Coxae, legs black, distal articles dusky orange, posterior two leg pairs ringed. Dorsum of abdomen black with three indistinct white lines (Fig. 523); venter black with two parallel white lines. Secondary eyes 0.7 diameter of anterior medians. Anterior median eyes slightly less than their diameter apart; posterior median eyes slightly more than their diameter apart. Fourth legs slightly longer than the first; second tibiae without macrosetae and not swollen. Abdomen elongate, oval, with posterior hump (Fig. 523). Total length 5.2 mm. Carapace 2.1 mm long, 1.5 wide. First femur 2.1 mm; patella and tibia 2.4; metatarsus 1.5; tarsus 0.7. Second patella and tibia 1.9 mm; third 1.7; fourth 2.5.

Note. This male may belong to *A. muco,* but the species' collecting sites are far apart.

Diagnosis. Unlike any other *Alpaida,* the median apophysis has a set off piece with three tips and the distal end of the terminal apophysis has a long saber-shaped projection (Fig. 524).

Alpaida albocincta (Mello-Leitão), new combination
Figures 525–529; Map 5

Epeirella albocincta Mello-Leitão, 1945: 236. Immature female holotype from Puerto Victoria, Misiones, Argentina (MLP), examined.

Note. Brignoli (1983) cited the species from Guyana and provided erroneous date and citation.

Description. Female. Carapace, sternum, legs yellowish. Dorsum of abdomen yellowish, white around sides, with faint black spot on posterior tip. Sides white. Venter dirty yellowish with some white pigment spots along center line. Abdomen truncate anterior with lateral grooves (Fig. 527). Total length 5.0 mm. Carapace 2.0 mm long, 1.7 wide. First femur 1.8 mm; patella and tibia 2.0; metatarsus 1.3; tarsus 0.7. Second patella and tibia 1.7; third 1.3; fourth 1.8.

Male. Coloration as in female (Fig. 528). Second tibiae thicker than others and with macrosetae. Total length 3.5 mm. Carapace 1.7 mm long, 1.5 wide. First femur

1.8 mm; patella and tibia 1.9; metatarsus 1.3; tarsus 0.7. Second patella and tibia 1.5 mm; third 1.1; fourth 1.6.

Variation. Total length females varies from 4.2 to 5.0 mm, males from 2.9 to 3.8. The lateral ends of the posterior median plate may be sclerotized dark or light (Fig. 526).

The female and male described and illustrated are from Rio Grande do Sul (MCN).

Diagnosis. Females are distinguished by the lateral grooves on the abdomen (Fig. 527) and also by the convex lobes on each side of the posterior median plate (Fig. 526). The males are distinguished by the deep median apophysis and the three pronged terminal apophyses, the basal prong and two distal ones pointing at each other (Fig. 529).

Records. VENEZUELA *Aragua*: Rancho Grande, 23 Aug. 1946, ♂ (W. Beebe, AMNH). BRAZIL *Rio Grande do Sul*: Montenegro, 15 Dec. 1977, ♀ (E. H. Buckup, MCN), 10 Nov. 1977, 6♂, ♀ (E. H. Buckup, MCN 6639), 6 Oct. 1977, ♂ (A. A. Lise, MCN 6832); Muçum, 2 Mar. 1984, 2♂ (A. D. Brescovil, MCN 12118). ARGENTINA *Misiones*: Eldorado, 1964, ♀ (A. Kovacs, AMNH).

Alpaida quadrilorata (Simon), new combination

Plate 1; Figures 530–536; Map 5

Araneus quadriloratus Simon, 1897c: 5. Female holotype from Asunción, Paraguay (MNHN), examined. Bonnet, 1955: 579.

Aranea quadrilorata:—Roewer, 1942: 850.

Cercidia octomaculata Mello-Leitão, 1945: 236, fig. 10, ♀. Female holotype from Pindapoy, Prov. Misiones, Argentina (MLP), examined, NEW SYNONYMY.

Parepeira ocellifera Mello-Leitão, 1945: 241, fig. 19, ♂. Male holotype from Mburucuya, Prov. Corrientes, Argentina (MLP), examined, NEW SYNONYMY.

Alpaida ocellifera:—Brignoli, 1983: 256.

Alpaida octomaculata:—Brignoli, 1983: 256.

Description. Female. Carapace orange. Sternum orange with a median black streak. Legs orange with wide black rings. Dorsum of abdomen with four black, longitudinal bands, white in between, orange on each side anteriorly (Fig. 532); venter with two black bands, white in middle (Fig. 534). Fourth legs longer than first. Abdomen oval, pointed behind. Total length 11.6 mm. Carapace 5.0 mm long, 3.6 wide. First femur 3.1 mm; patella and tibia 4.2; metatarsus 2.3; tarsus 1.1. Second patella and tibia 3.7 mm; third 2.6. Fourth femur 3.2 mm; patella and tibia 4.2; metatarsus 2.6; tarsus 1.0.

Male. Coloration as in female, but legs darker. Abdomen with orange disks and two median dorsal black stripes (Fig. 535). Second tibiae thick with strong macrosetae. Abdomen sclerotized, with dorsal sclerotized disks. Total length 9.1 mm. Carapace 4.5 mm long, 3.4 wide. First femur 3.4 mm; patella and tibia 4.1; metatarsus 2.5; tarsus 1.0. Second patella and tibia 3.6 mm; third 2.4; fourth 3.4.

Variation. Total length of females varies from 10.7 to 13.6 mm, of males from 8.9 to 9.5. Females are marked with black patches on the abdomen (Fig. 533) or longitudinal bands. Frequently both kinds of females are collected together. The background of stripes or patches varies from white to dark orange in alcoholic specimens. A male from Pelotas, Rio Grande do Sul, was all black.

The female and male illustrated and described are from Rio Grande do Sul (MCZ).

Diagnosis. The markings on the abdomen in both sexes (Figs. 532–535) separate the species from *A. angra* and other *Alpaida*. The epigynum is triangular with an indistinct lip (Fig. 530), the palpus has a long median apophysis, and both the embolus and basal prong of the embolus are curved, with their tips approaching each other (Fig. 536).

Natural History. Immature individuals have been collected from a tiny web in agave on a dry hillside at Port Alegre (Plate 1), adults are collected on the thistle-like umbellifer *Eryngium horridum* (A. A. Lise, personal correspondence). Collections from Paraguay came from the same species of plant. Kochalka (in letter) wrote that the web is always in the center of the plant,

the spider in the hub during the day. The plant grows in sunny places in wet soil. These plants usually have trapped water among the bases of leaves. When disturbed, the spiders submerge. "As far as I am aware, this is the only *Alpaida* that goes under water . . . the spider goes in head first and wedges itself so tightly into the base of the leaf, that one must destroy the plant to get the spider out. I have divided *A. quatrilorata* into three color varieties. I think they are separate species."

Records. BRAZIL *Minas Gerais*: Serra do Caraça (MZSP 6715). *São Paulo*: Cámpos do Jordão (MZSP 4407); Ipiranga (MZSP 5792). *Paraná*: Curitiba (MZSP 3017, 4976). *Rio Grande do Sul*: Montenegro (MCN); Pelotas (MCN); Gravatai (MCZ); Garruchos, São Borja (MCN); Triunfo (MCN); Porto Alegre (MCN, MNRJ). URUGUAY *Lavaleja*: Asperezas del Polanco (MHNM). *Artigas*: Arroyo Tres Cruces (MHNM). *Treinta y Tres*: Santa Clara de Olimar (MHNM). PARAGUAY *Paraguarí*: Cerro Acahay, Colonia Virgen de Fátima (MNHNP); Sapucaí (MNHNP, MCZ). *Central*: Luque (MNHNP). *Concepcíon*: Territ. Fonciére (MCZ). ARGENTINA *Misiones*: San Pedro (MACN). *Corrientes*: Corrientes (MACN). *Buenos Aires*: Buenos Aires (MACN).

Alpaida angra new species
Figures 537–540; Map 5

Holotype. Female holotype and five female paratypes from Angra dos Reis, Est. Rio de Janeiro, Brazil, 28 Dec. 1951 (L. Travassos Filho and Rabello, MZSP no. 6818). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, sternum, coxae orange. Legs black. Dorsum of abdomen black, white and orange (Fig. 539); venter with central white patch on orange and a posterior transverse black band including the spinnerets (Fig. 540). Anterior median eyes their diameter apart; posterior median eyes 1.3 times their diameter apart. Abdomen oval. Total length 9.4 mm. Carapace 3.9 mm long, 3.2 wide. First femur 3.1 mm; patella and tibia 3.9; metatarsus 2.5; tarsus 1.2. Second patella and tibia 3.4 mm; third 2.4; fourth 3.7.

Diagnosis. This species is distinguished from *A. quadrilorata* by a black band through the median of the abdomen (Fig. 539) and an epigynum with a longer lobe, making the epigynum as wide as long in ventral view (Fig. 537).

Paratype. BRAZIL *São Paulo*: Itanhaém, Nov. 1925 (R. Spitz, MZSP 5469).

Alpaida darlingtoni new species
Figures 541–546; Map 5

Holotype. Female holotype with male and juvenile male paratypes from Cerro Pulmado, 2,500–2,800 m, northwestern Sierra Nevada de Santa Marta, Colombia, 25 Sept. 1928 (P. J. Darlington, MCZ). The species is named after the collector.

Description. Female. Carapace, sternum, legs orange. Dorsum of abdomen white with a posterior pair of black spots (Fig. 543); venter orange. Abdomen oval, with lateral grooves (Fig. 543). Total length 4.9 mm. Carapace 2.1 mm long, 1.6 wide. First femur 1.9 mm; patella and tibia 2.3; metatarsus 1.7; tarsus 0.9. Second patella and tibia 2.0 mm; third 1.1; fourth 1.8.

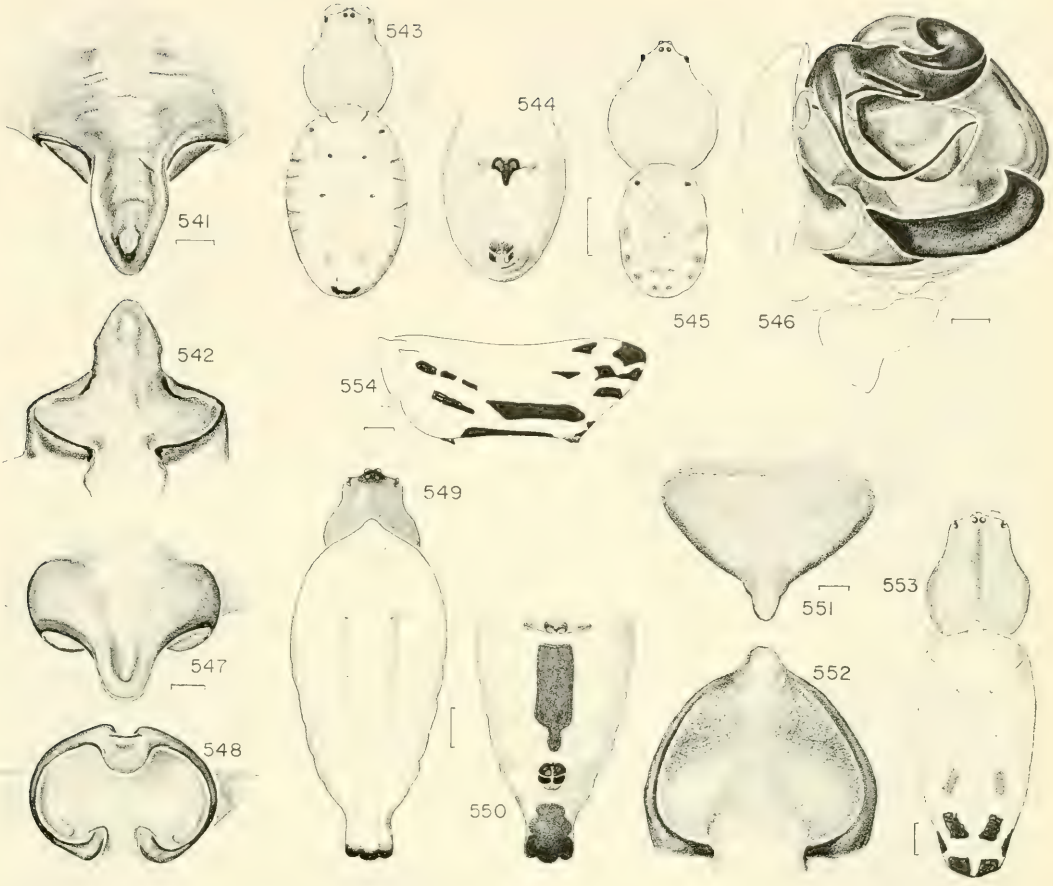
Male. Coloration as in female (Fig. 545). Second tibiae with macrosetae, fourth trochanters with a macroseta. Total length 4.2 mm. Carapace 2.2 mm long, 1.9 wide. First femur 2.0 mm; patella and tibia 2.5. Second femur 1.8 mm; third 1.1; fourth 1.9.

Diagnosis. The female distinguished from other *Alpaida* species by the longer than wide epigynum with a scape that is slightly constricted at its base (Fig. 541). The palpus, unlike others, has a filiform embolus with the distal lobe of the terminal apophysis forming a hook, its tip pointing at the cymbium (Fig. 546).

Alpaida madeira new species
Figures 547–550; Map 5

Holotype. Female from Rio Madeira, Pôrto Velho, Est. Rondônia, Brazil (Stanford Exped., W. M. Mann, ex MCZ, MZSP). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange, median eye region black. Sternum, coxae



Figures 541–546. *Alpaida darlingtoni* n. sp., female. 541, epigynum, ventral. 542, epigynum, posterior. 543, dorsal. 544, ventral. 545, 546, male. 545, dorsal. 546, left palpus.

Figures 547–550. *A. madeira* n. sp., female. 547, epigynum, ventral. 548, epigynum, posterior. 549, dorsal. 550, ventral.

Figures 551–554. *A. roemeri* (Strand), female. 551, epigynum, ventral. 552, epigynum, posterior. 553, dorsal. 554, lateral.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

orange. Second femora, distal half of other and distal articles black with orange ring proximally on tibia. Dorsum of abdomen white with tip of tail black (Fig. 549); venter with black rectangle, black spinnerets, black tail (Fig. 550). Abdomen elongated with tail basally constricted. Total length 10.0 mm. Carapace 2.9 mm long, 2.5 wide. First femur 3.7 mm; patella and tibia 4.3; metatarsus 3.1; tarsus 1.2. Second patella and tibia 3.4 mm; third 2.4; fourth 4.0.

Diagnosis. Females, unlike other *Alpaida*, have a tail, slightly constricted at its base and with three distal lobes, on the abdomen (Figs. 549, 550). The epigynum is distinguished from that of *A. quadrilorata* by a slight median longitudinal groove (Figs. 547, 548).

Alpaida roemeri (Strand), new combination

Figures 551–554; Map 5

Aranea roemeri Strand, 1908: 3. Female holotype from Joinville [Joinvile], Santa Catarina, Brazil (SMF), examined. Roewer, 1942: 851.

Araneus roemeri:—Bonnet, 1955: 586.

Note. The abdomen of the holotype is damaged.

Description. Female. Carapace brown with a median longitudinal dark line and thoracic border dark. Sternum, legs light brown; legs with contrasting dark brown rings. Dorsum of abdomen and sides with black patches on posterior (Fig. 553); sides with black patches, black between genital groove and spinnerets (Fig. 554); spinnerets dark brown; paired black patches on overhang behind spinnerets. Anterior median eyes 1.5 diameters apart, posterior median eyes 1.5 diameters apart. Abdomen [damaged] probably with three humps anteriorly, much longer than wide, with tail overhanging spinnerets (Fig. 554). Total length 12.0 mm. Carapace 4.1 mm long, 3.5 wide. First femur 4.2 mm; patella and tibia 4.5; metatarsus 3.4; tarsus 1.4. Third patella and tibia 2.6 mm; fourth 4.3.

Diagnosis. This species is distinguished from others by the slight constriction near the posterior end of the abdomen (Fig. 553). The epigynum differs from that of *A. madeira* by having only a small median lobe and being subtriangular in median and posterior views (Figs. 551, 552).

Alpaida eberhardi new species
Figures 555–558; Map 5

Holotype. Female from 25 km W of Queremal, Dpto. Valle, Colombia, 1977, (W. Eberhard, MCZ). The species is named after the collector.

Description. Female. Carapace, yellowish. Labium, endites, sternum, black. Legs yellowish with wide dusky rings. Dorsum of abdomen with white patches (Fig. 557); sides with dorsal longitudinal black band and ventral white area; venter black (Fig. 558). Abdomen elongate rounded in front, pointed behind (Fig. 557). Total length 4.7 mm. Carapace 1.9 mm long, 1.5 wide. First femur 1.9 mm; patella and tibia 2.5; metatarsus 1.5; tarsus 0.7. Second patella and tibia 2.2 mm; third 1.2; fourth 2.1.

Variation. Total length from 3.8 to 4.8 mm. The holotype was described and illustrated.

Diagnosis. The epigynum differs from that of most *Alpaida* by having an edge along its anterior face in ventral view and from that of *A. machala* by having a longer, narrower median lobe (Figs. 555, 556).

Paratypes. COLOMBIA *Antioquia*: Mutatá "Cancheras" 6 Dec. 1963, ♀ (P. B. Schneble, MCZ). *Valle*: Central Hidroelectrica Anchicayá, Canyon Río Anchicayá, 400 m, 1975, ♀, 1977, ♀ (W. Eberhard, MCZ).

Alpaida machala new species
Figures 559–563; Map 5

Holotype. Female from Buenavista, 20 km SE of Machala, Prov. El Oro, Ecuador, 1–20 Nov. 1942 (R. Walls, CAS). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellow; labium, endites dusky; sternum black. Coxae and legs yellow. Dorsum of abdomen with white pigment, with dusky marks on shoulder, dusky transverse band posteriorly (Fig. 562); sides with a dusky band between two white bands; venter black from genital groove to behind spinnerets (Fig. 563). Abdomen rounded anteriorly, slightly pointed posteriorly [abdomen damaged]. Total length 3.8 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.9 mm; patella and tibia 2.1; metatarsus 1.4; tarsus 0.7. Second patella and tibia 1.9 mm; third 1.1; fourth 1.8.

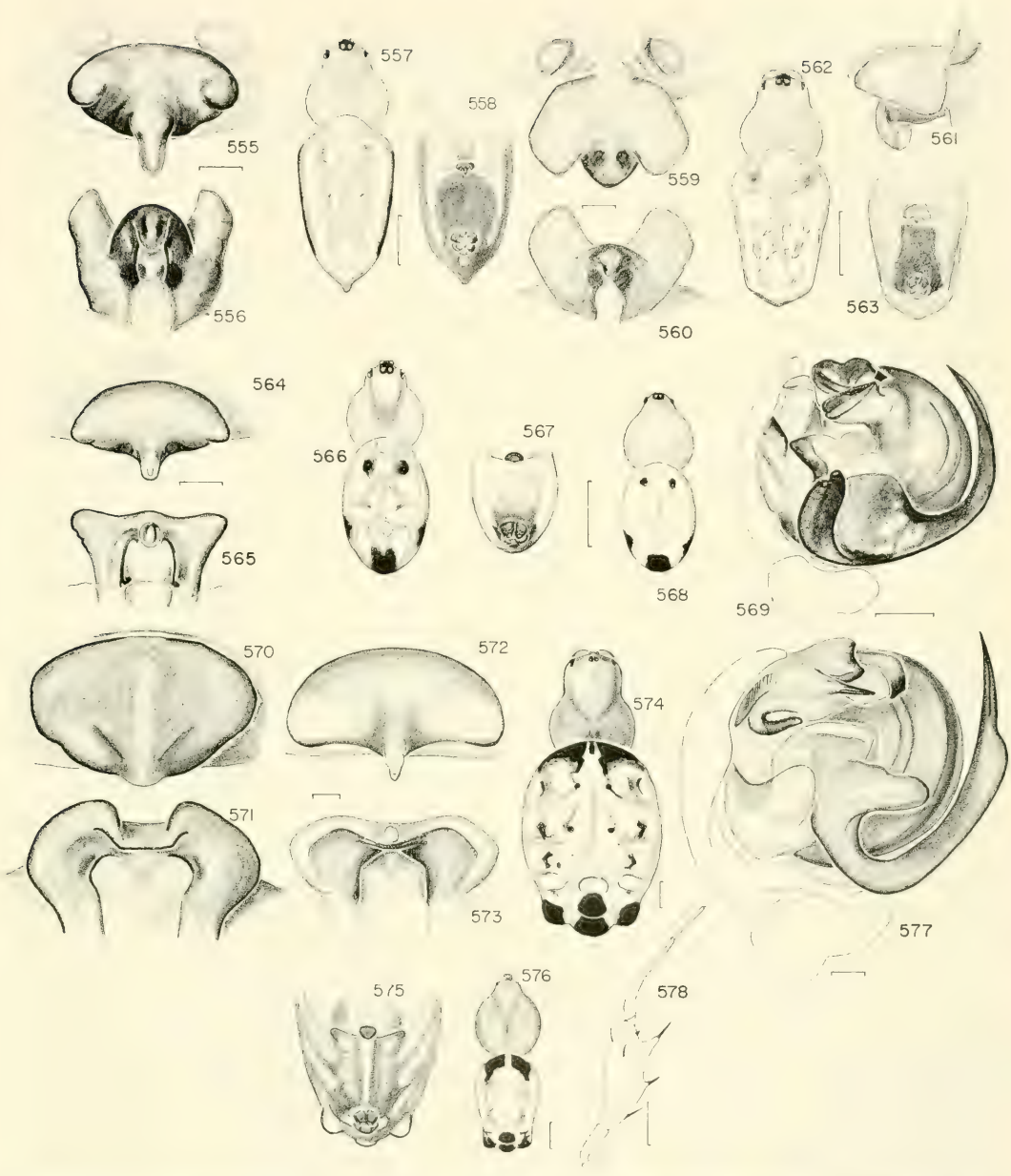
Diagnosis. The epigynum of the female differs from that of *A. eberhardi* by having the median lobe wider at its base and the lateral lobes longer (Figs. 559–561). Also, the anterior margin of the epigynum is broken in the midline (Fig. 559).

Paratype. ECUADOR *Pichincha*: 35 km NW Santo Domingo de los Colorados, 22 Dec. 1958, 2♀ (A. M. Nadler, AMNH).

Alpaida queremal new species
Figures 564–569; Map 5

Holotype. Female from Río San Juan, afl. del Digua near Queremal, 1,300 m, Dpto. Valle, Colombia, 1976 (W. Eberhard, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellow-white with thorax dusky; labium, endites,



Figures 555–558. *Alpaida eberhardi* n. sp., female. 555, epigynum, ventral. 556, epigynum, posterior. 557, dorsal. 558, ventral.

Figures 559–563. *A. machala* n. sp., female. 559, epigynum, ventral. 560, epigynum, posterior. 561, epigynum, lateral. 562, dorsal. 563, ventral.

Figures 564–569. *A. queremal* n. sp. 564–567, female. 564, epigynum, ventral. 565, epigynum, posterior. 566, dorsal. 567, ventral. 568, 569, male. 568, dorsal. 569, left palpus.

Figures 570–578. *A. truncata* (Keyserling). 570–575, female. 570, 572, epigynum, ventral. 571, 573, epigynum, posterior. 570, 571, (Paraguay). 572, 573, (Panama). 574, dorsal. 575, ventral. 576–578, male. 576, dorsal. 577, palpus. 578, second left leg, dorsal.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

dusky. Sternum, black. Legs, yellow-white. Dorsum of abdomen with paired white patches, a pair of black patches anteriorly, and a posterior median black patch (Fig. 566); sides with a dorsal posterior black mark and ventral white band; venter, dusky, black around spinnerets (Fig. 567). Abdomen oval. Total length 3.2 mm. Carapace 1.4 mm long, 1.1 wide. First femur 1.6 mm; patella and tibia 1.8; metatarsus 1.1; tarsus 0.5. Second patella and tibia 1.5 mm; third 1.0; fourth 1.4.

Male. Color as in female (Fig. 568). Total length 2.7 mm. Carapace 1.3 mm long, 1.1 wide. First femur 1.6 mm; patella and tibia 1.7; metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.3 mm; third 0.9; fourth 1.2.

Variation. Total length of females varies from 3.2 to 3.5 mm. Female from Dpto. Nariño has carapace olive-white without dusky areas, the dorsum of the abdomen with sides and posterior golden yellow on white, an anterior golden yellow patch, middle without pigment, black on each shoulder, and a pair of black patches posterior. Endites, labium, sternum and venter of abdomen black.

The female holotype is described and illustrated.

Diagnosis. This species is much smaller than *A. truncata* and the abdomen is rounded behind and lacks the four humps on the posterior (Figs. 566, 567). Unlike *A. truncata*, the epigynum has two projecting ventral lateral lobes (Figs. 564, 565) and the median apophysis of the male palpus lacks the notch in the base present in *A. truncata* (Fig. 569).

Paratypes. COLOMBIA *Nariño*: La Planada, 1,800 m, 7 km S Choconés, nr. Ricaurte, July 1986, 3♀, 6♂ (W. Eberhard FN8-29F, MCZ).

Alpaida truncata (Keyserling), new combination

Plates 1, 2; Figures 570–578; Map 5

Epeira truncata Keyserling, 1865: 807, pl. 19, fig. 21, ♀. Female from Uruguay (BMNH), examined.

Epeira elegantissima Taczanowski, 1878: 170, pl. 2, fig. 19. ♀. Female from Amable María, [Dpto. Junín], Peru (PAN), examined.

Epeira cylindrica Taczanowski, 1878: 171, pl. 2, fig. 20, 21, ♀, ♂. Male lectotype here designated from Amable María, [Dpto. Junín], Peru (PAN), examined.

Epeira nigropustulata O. P.-Cambridge, 1893: 111, pl. 15, fig. 5, ♀. Female from Teapa, Tabasco, Mexico (BMNH), examined. NEW SYNONYMY.

Aranea nigropustulata:—F. P.-Cambridge, 1904: 516, pl. 49, fig. 22, ♀.

Araneus mutatus Chamberlin and Ivie, 1936: 46, pl. 14, fig. 128, 129, ♀. Female from Barro Colorado Island, Panama (AMNH), examined. Bonnet, 1955: 547. NEW SYNONYMY.

Edricus truncatus:—Roewer, 1942: 762. Bonnet, 1956: 1649.

Epeiroides albonotatus Mello-Leitão, 1945: 237. Early instar, immature from Misiones Prov., Argentina (MULP), examined. Brignoli, 1983: 268. NEW SYNONYMY.

Edricus ensifer Caporiacco, 1947: 25; 1948: 658, fig. 66, ♂. Male holotype from Two Mouths, Essequebo River, British Guyana (MZUF), examined. NEW SYNONYMY.

Subedricus nigropustulata:—Caporiacco, 1954: 84.

Description. Female. Carapace, sternum, legs brown. Dorsum of abdomen white and black (Fig. 574); venter with median white streak (Fig. 575). Abdomen oval, posterior truncate with four humps (Fig. 574). Total length 10.7 mm. Carapace 4.2 mm long, 3.4 wide. First femur 3.9 mm; patella and tibia 4.9; metatarsus 3.1; tarsus 1.5. Second patella and tibia 4.5 mm; third 2.7; and fourth 4.7.

Male. Coloration as in female but carapace, sternum and legs lighter brown (Fig. 576). Tibia of second leg flattened and wide (Fig. 578). Shape of abdomen like that of female. Total length 6.2 mm. Carapace 3.1 mm long, 2.4 wide. First femur 3.4 mm; patella and tibia 4.2; metatarsus 2.5; tarsus 1.2. Second patella and tibia 3.5 mm; third 2.0; and fourth 3.6.

Variation. Total length of females varies from 8.3 to 12.8 mm, of males from 4.8 to 8.2. Some individuals are all black. A living specimen had carapace and legs a transparent orange, abdomen bright yellow with shiny black patches (Plate 1).

The female and male illustrated and described are from Paraguay (MCZ).

Diagnosis. Both sexes differ from all

other *Alpaida* by having the abdomen truncate posteriorly with black humps (Figs. 574–576), and also differ from *A. queremal* by being larger. The female, unlike *A. queremal* lacks the lateral lobes of the epigynum (Figs. 570, 571). The male, unlike other *Alpaida*, has a modified second tibia, flattened and wide, bearing two macrosetae (Fig. 578) and is distinguished from *A. queremal* by a notch in the base of the median apophysis of the palpus (Fig. 577).

Natural History and Distribution. The species has been collected from forest in Pará and Minas Gerais, Brazil, and from gallery forest in Mato Grosso.

Alpaida truncata do not usually have a free sector in the web (Plate 2) but have a signal line out of the web plane and an intact orb. The posterior ends of their abdomens are brightly colored. The spiders sit in the retreat facing away from the orb and hold the signal line with a leg four. Kochalka (in letter) wrote that in Paraguay, *A. truncata* is found in a rolled green leaf during the day. The black spots on the abdomen look like eyes when seen through the opening of the retreat, which is usually 1 to 2 m above the ground in humid forest and quite small. All coxae, third and fourth femora, and ventrolateral stripes on the abdomen are green. The green fills in the space between eyespots and spinnerets. *A. truncata* is found from southern Mexico to northern Argentina (Map 5).

Records. COSTA RICA *Heredia*: La Selva, nr. Puerto Viejo (MCZ). *Cartago*: Turrialba (MCZ). PANAMA *Panamá*: Arraijan (MCZ); Forest Reserve (MCZ); Barro Colorado Isl., Lago Gatún (AMNH). LESSER ANTILLES *Trinidad*: Coparo (AMNH). VENEZUELA *Carabobo*: San Esteban (AMNH). *Bolivar*: Hato La Vergareña (AMNH). *Amazonas*: Prov. la Esmeralda, Alto Orinoco (MCZ). SURINAM *Saramacca*: Voltzberg—Raleighvallen Nature Reserve (MCZ). *Marowijne*: Christian Kondre (AMNH). COLOMBIA *Santander*: Río Suárez, 800–1,000 m (AMNH). *Cundinamarea*: Monterredondo, 1,200 m (MCZ). *Meta*: Puerto Lleras (MCZ); 15 km SW Puerto López, 500 m, (MCZ). *Putumayo*: Pto. Asis (MCZ). ECUADOR *Napo*: Cuyabene (L. Grande) (MECN). *Monrona-Santiago*: Los Trayos (MCZ); Sucúa (MCZ). *Los Ríos*: Juan Montalvo (AMNH); SW Queveda (CAS). PERU *Loreto*: Iquitos (MCZ). *San Martín*: 32 km SE Moyobamba (AMNH). *Huánuco*: Tingo María (AMNH). *Cuzco*: Quillabamba, 1,000 m (AMNH). BRAZIL *Pará*: Belém (MEG, MCZ); Canindé, Rio Gurupi (AMNH). *Amazonas*: Benjamin Constant (MNRJ); Igarape Belém (AMNH); Fonte Bôa (AMNH); Manaus (NHRM); mouth of Rio Embira, Rio Juruá (AMNH). *Bahia*: Salvador (AMNH); Uruçuca (MCN). *Mato Grosso*: 260 km N Xavantina (MCZ); Chapada dos Guimaroes (AMNH). *Minas Gerais*: Lavras (MCZ); Aripuana (MCZ). *Espírito Santo*: Sosretame Linhares (MZSP). *Rio de Janeiro*: Rio de Janeiro (AMNH). *São Paulo*: Faz Itaqueri (MCN). *Paraná*: Rio Negro (MNRJ). *Rio Grande do Sul*: Triunfo (MCN). BOLIVIA *El Beni*: Chacobo Indian Village, Río Benito (AMNH). PARAGUAY *Concepción*: Apa (AMNH). *Central*: San Lorenzo (MNHNP). *Paraguarí*: Parque Nac. Ybyouí (MNHNP). *Caaguazú*: Colón (MNHNP). ARGENTINA *Misiones*: San Ignacio (MEG); Misiones (MACN); Puerto Victoria (MLP); Dpto. San Antonio (MEG); *Chaco*: Selva del Río de Oro (MEG).

Alpaida yotoco new species
Figures 579–582; Map 5

Holotype. Female from Yotoco, 1,500 m, Dpto. Valle, Colombia, Aug. 1977 (W. E. Eberhard no. 1217, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, yellowish. Labium, endites, sternum, black. Legs yellowish, distal articles dusky. Dorsum of abdomen with white patches (Figs. 581), lateral white patches yellowish; sides dusky; venter, black sides with tiny white spots (Fig. 582). Abdomen elongate oval with anterior median hump and posterior point (Fig. 581). Total length 4.3 mm. Carapace

1.5 mm long, 1.3 wide. First femur 1.7 mm; patella and tibia 1.9; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.6 mm; third 1.1; fourth 1.6.

Variation. Total length of females varies from 3.5 to 4.3 mm.

Diagnosis. This species is distinguished from *A. nadleri* by the epigynum which, in posterior view, has a lip as wide or wider than the median plate (Fig. 580).

Paratype. COLOMBIA *Valle*: nr. Yotoco, 1,600 m, Dec. 1976, ♀ (W. Eberhard, MCZ).

Alpaida nadleri new species
Figures 583–586; Map 5

Holotype. Female from Rancho Grande, Prov. Aragua, Venezuela, 20 Dec. 1954 (A. M. Nadler, AMNH). The species is named after the collector.

Description. Female. Carapace, sternum, legs yellowish. Dorsum of abdomen with white patches and two pairs of black patches (Fig. 585); venter with black patch between epigynum and spinnerets. Eyes small. Anterior median eyes 1.8 diameters apart; posterior median eyes 1.4 diameters. Abdomen rounded anteriorly and posteriorly. Total length 3.4 mm. Carapace 1.5 mm long, 1.3 wide. First femur 1.8 mm; patella and tibia 2.1; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.7 mm; third 1.1; fourth 1.6.

Diagnosis. The species is distinguished from *A. yocoto* by the curved lips near the midline in posterior view of the epigynum (Fig. 584).

Paratype. VENEZUELA *Aragua*: Rancho Grande, March 1946, ♀ (W. Beebe, AMNH).

Alpaida anchicaya new species
Figures 587–592; Map 5

Holotype. Male holotype and female paratype from Central Hidroelectrica Anchicayá, Canyon Río Anchicayá, 400 m, near road to Buenaventura, Dpto. Valle, Colombia, 24 April 197? (W. Eberhard, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellowish, eye region black. Chelicerae yellowish, distally black; labium, endites, sternum black. Legs yellowish, darker distally. Dorsum of abdomen with black and white pigment (Fig. 589); venter with wide median longitudinal black band (Fig. 590). Abdomen oval. Total length 2.5 mm. Carapace 1.23 mm long, 0.91 wide. First femur 1.36 mm; patella and tibia 1.53; metatarsus 1.00; tarsus 0.57. Second patella and tibia 1.24; third 0.78; fourth 1.20.

Male. Coloration as in female (Fig. 591). Second tibiae not swollen. Total length 2.1 mm. Carapace 1.14 mm long, 0.97 wide. First femur 1.63 mm; patella and tibia 1.78; metatarsus 1.11; tarsus 0.62. Second patella and tibia 1.37 mm; third 0.89; fourth 1.30.

Diagnosis. Females are distinguished from *A. cisneros* by two proximal notches on the epigynum, visible in posterior view (Fig. 588). The male, unlike most *Alpaida*, has the median apophysis of the palpus drawn out beyond the bulb as in *A. queremal* and *A. truncata*, but differs from these two species by having a filiform embolus lying "on top" of the bulb (Fig. 592).

Paratypes. COLOMBIA *Valle*: Central Hidroelectrica Anchicayá, 400 m, 4♀; 1977, ♀, 2♂; 1978, ♂ (all W. Eberhard, MCZ).

Alpaida tuonabo (Chamberlin and Ivie)
Figures 593–598; Map 5

Araneus tuonabo Chamberlin and Ivie, 1936: 50, pl. 14, fig. 130, ♀. Female holotype from Barro Colorado Island, Panama (AMNH), examined. Bonnet, 1955: 620. Lubin, 1978.

Aranea tuonabo:—Roewer, 1942: 854.

Alpaida tuonabo:—Shelly, 1983: 123. Eberhard, 1986: 73, fig. 4.2f (web).

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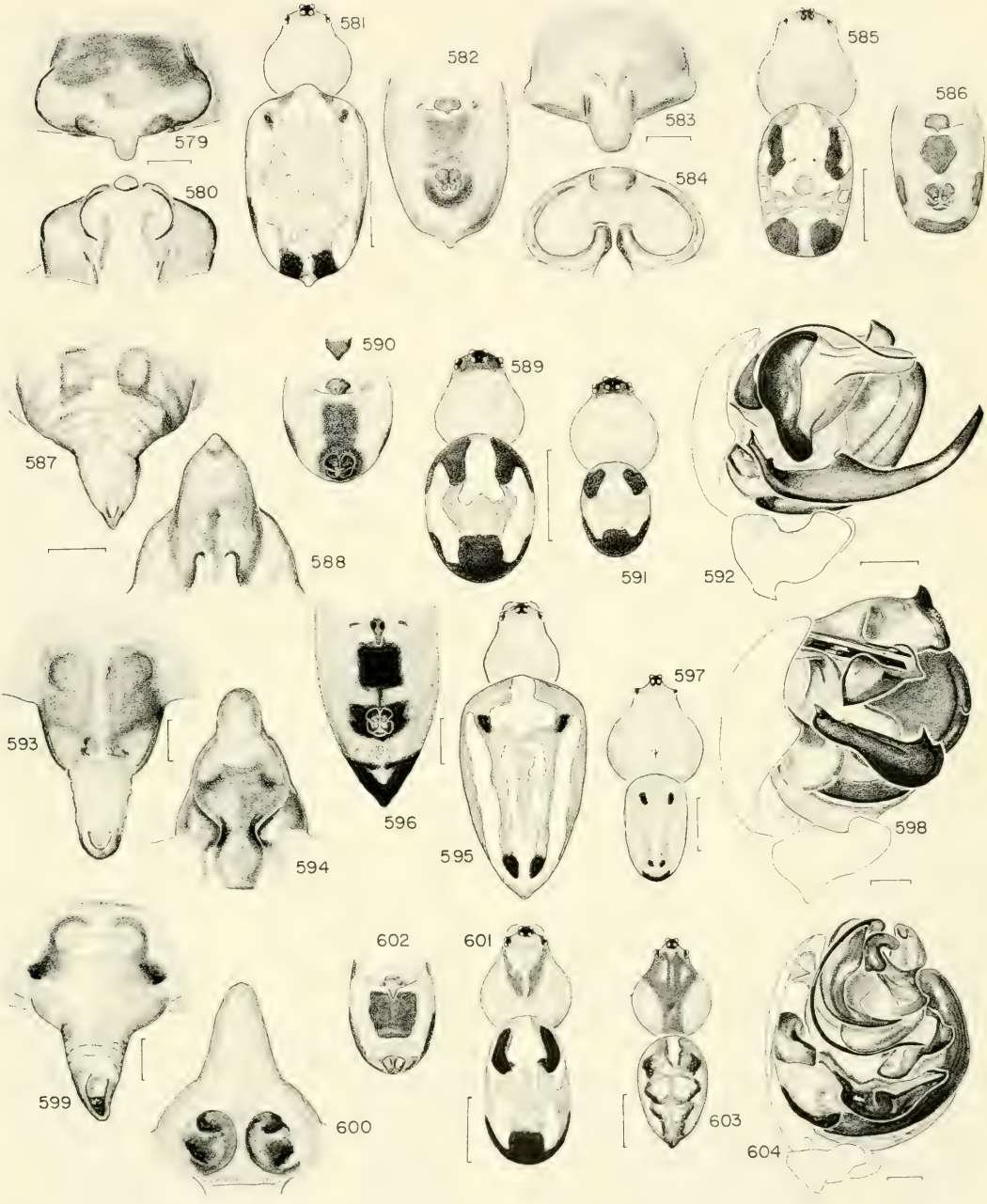
Figures 579–582. *Alpaida yotoco* n. sp., female. 579, epigynum, ventral. 580, epigynum, posterior. 581, dorsal. 582, ventral.

Figures 583–586. *A. nadleri* n. sp., female. 583, epigynum, ventral. 584, epigynum, posterior. 585, dorsal. 586, ventral.

Figures 587–592. *A. anchicaya* n. sp. 587–590, female. 587, epigynum, ventral. 588, epigynum, posterior. 589, dorsal. 590. ventral. 591, 592, male. 591, dorsal. 592, left palpus.



Figures 593–598. *A. tuonabo* (Chamberlin and Ivie). 593–596, female. 593, epigynum, ventral. 594, epigynum, posterior. 595, dorsal. 596, ventral. 597, 598, male. 597, dorsal. 598, palpus.

Figures 599–602. *A. cisneros* n. sp., female. 599, epigynum, ventral. 600, epigynum, posterior. 601, dorsal. 602, ventral.

Figures 603, 604. *A. schneblei* n. sp., male. 603, dorsal. 604, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

Description. Female. Carapace colorless, whitish; sternum yellow. Legs colorless, ringed black; first and second patella and tibia black. Dorsum of abdomen with yellow-white bands separated by pigmentless area and four black patches (Fig. 595); venter with black patch, black around spinnerets and under tail (Fig. 596). Abdomen elongate (Fig. 595). Total length 6.7 mm. Carapace 2.1 mm long, 1.8 wide. First femur 2.5 mm; patella and tibia 2.8; metatarsus 1.7; tarsus 0.7. Second patella and tibia 2.5 mm; third 1.5; fourth 2.3.

Male. Carapace colorless to whitish. Legs blackish. Dorsum of abdomen yellowish-white with four black spots and black on posterior margin (Fig. 597); venter black in center, black around and behind spinnerets. Fourth coxae with one or two short macrosetae. Abdomen shorter than that of female. Total length 4.0 mm. Carapace 2.0 mm long, 1.8 wide. First femur 2.5 mm; patella and tibia 2.6; metatarsus 1.6; tarsus 0.7. Second patella and tibia 2.1 mm; third 1.3; fourth 2.1.

Variation. Females vary in total length from 4.1 to 6.7 mm, males from 3.5 to 4.0. A photograph of a living specimen had yellow patches on a dark dusky orange background with black marks.

Diagnosis. Females are distinguished from most *Alpaida* by the longer than wide epigynum with a wide scape (Fig. 593), and from *A. cisneros* in posterior view by a narrow lip with a proximal swelling (Fig. 594). Males distinguished from other species by the long median apophysis with one tooth on the proximal end and two teeth on the distal end (Fig. 598).

Natural History and Distribution. The species is very common in the Panama Canal area in open areas in lowland tropical moist forest from July to December, during the mid to late wet season. Females make and tend webs during the day and consume them at night. Web sites are shaded. Webs average 21.6 cm in diameter and are supported by herbaceous stems, woody vines and branches at a height of 0.6 to 1.2 m. Individuals move to another web site after one to two days. The spiders feed on various small insects (Lubin, 1978; Shelly, 1983). Eberhard (1986) illustrated the web.

Records. PANAMA *Colón*: Portobelo (MCZ); Fort Gulick (AMNH); Fort Sherman (AMNH). *Panamá*: Pipeline Road (MCZ, MIUP); Barro Colorado Island, Lago Gatún (MCZ, AMNH); Experimental Gardens (MCZ); Gamboa (AMNH); El Valle (MCZ).

Alpaida cisneros new species
Figures 599–602; Map 5

Holotype. Female from near Cisneros, 500 m, Dpto. Valle, Colombia, April 1976 (W. Eberhard no. 1089, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellow-white with a pair of dark marks. Labium, endites, sternum, black. Legs yellow-white. Dorsum of abdomen with black and white patches (Fig. 601); venter with median black patch (Fig. 602). Legs with a short dorsal macrosetae on each femur, several on inside of first. Total length 3.6 mm. Carapace 1.7 mm long, 1.5 wide. First femur 2.0 mm; patella and tibia 2.3; metatarsus 1.6; tarsus 0.8. Second patella and tibia 1.9 mm; third 1.3; fourth 1.9.

Variation. Females vary in total length from 3.4 to 4.7 mm. The largest specimen comes from Ecuador.

The female holotype was described and illustrated.

Diagnosis. This species is distinguished from *A. tuonabo* by the point on the scape of the epigynum (Fig. 599) and in posterior view by the dark seminal receptacles visible through the transparent integument (Fig. 600).

Paratypes. COLOMBIA *Valle*: 20 km E of Buenaventura, 1974, ♀ (W. Eberhard, MCZ). *Cauca*: NW of Guapi, ca. 100 m, 3 Jan. 1973, ♀ (W. Eberhard, MCZ). ECUADOR *Pichincha*: Via Pto. Quito, km 113, 5 April 1985, ♀ (G. Morejon, MECN).

Alpaida schneblei new species
Figures 603, 604; Map 5

Holotype. Male from Mutatá "Cancheras," Dpto. Antioquia, Colombia, July, 1963 (P. B. Schneble, MCZ). The species is named after the collector.

Description. Male. Carapace yellowish with black patch in middle (Fig. 603). Labium, sternum, endites, black. Coxae, distal leg articles yellow-white with indistinct narrow dark rings. Dorsum of abdomen with white cardiac mark and white band on each side (Fig. 603); venter, black. Abdomen pointed posteriorly. Total length 4.0 mm. Carapace 1.9 mm long, 1.6 wide. First femur 1.7 mm; patella and tibia 2.0; metatarsus 1.2; tarsus 0.6. Second patella and tibia 1.6 mm; third 1.2; fourth 1.9.

Diagnosis. Although the male belongs to the group of *Alpaida* species with a white cardiac mark, the palpus, with its long filamentous embolus, resembles the palpus of *A. anchicaya* and *A. cali* and others, but is distinguished by the shape of the median apophysis and terminal apophysis (Fig. 604).

Alpaida silencio new species
Figures 605–610; Map 5

Holotype. Male holotype and female paratype from El Silencio, near Cali, 2,000 m, Colombia, July 1974 (W. Eberhard no. I-867, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace, legs light orange. Labium, endites, sternum black. Dorsum of abdomen with black and white pigment patches (Fig. 607); venter black around spinnerets, gray anteriorly with some white pigment (Fig. 608). Abdomen cylindrical (Fig. 607). Total length 3.8 mm. Carapace 1.6 mm long, 1.3 wide. First femur 1.8 mm; patella and tibia 2.0; metatarsus 1.3; tarsus 0.7. Second patella and tibia 1.8 mm; third 1.1; fourth 1.7.

Male. Coloration as in female (Fig. 609). Venter of abdomen mostly black. Second tibiae not swollen. Total length 3.2 mm. Carapace 1.6 mm long, 1.3 wide. First femur 1.9 mm; patella and tibia 2.0; metatarsus 1.3; tarsus 0.6. Second patella and tibia 1.6 mm; third 1.1; fourth 1.5.

Diagnosis. Females distinguished from *A. anchicaya* by a lateral swelling on each side of the median lobe (Fig. 605). The palpus of the male differs from *A. anchicaya* by having the drawn out distal end of the median apophysis curled back, its tip under the conductor (Fig. 610) and the embolus wide at its base with a filamentous tip "on top" of the bulb (Fig. 610).

Natural History. This species is found in cloud forest at high elevation.

Paratypes. COLOMBIA *Valle*: Saladito, 1,800 m, Oct. 1975, ♀ (W. Eberhard E149, MCZ); 3 Jan. 1977, ♀ (H. Levi, MCZ).

Alpaida cali new species
Figures 611–616; Map 5

Holotype. Female from Cali, Dpto. Valle, Colombia, 1,000 m, 1976 (W. Eberhard, MCZ). The specific name is a noun in apposition after the locality.

Description. Female. Carapace orange-yellow; sternum orange with median black spot. Legs orange-yellow, third and fourth legs with narrow black rings or spots. Dorsum of abdomen with black and white pigment on orange gray; sides with diagonal streak anteriorly continued ventrally, a black patch posteriorly (Fig. 613); venter with black patches on orange (Fig. 614). Posterior median eyes twice diameter of all others. Abdomen oval, scalloped on sides (Figs. 613, 614). Total length 4.0 mm. Carapace 1.5 mm long, 1.1 wide. First femur 1.3 mm; patella and tibia 1.5; metatarsus 1.1; tarsus 0.5. Second patella and tibia 1.3 mm; third 0.8; fourth 1.3.

Male. Color as in female. Dorsum of abdomen with three pairs of black patches and posterior black mark (Fig. 615); venter dusky. Abdomen oval. Total length 2.8 mm. Carapace 1.4 mm long, 1.1 wide. First femur 1.5 mm; patella and tibia 1.5; metatarsus 1.0; tarsus 0.5. Second patella and tibia 1.2 mm; third 1.0; fourth 1.5.

Variation. Males vary in total length from 2.8 to 3.3 mm.

Diagnosis. The epigynum is as long as wide or slightly longer, with a wide semicircular notch (Fig. 611), and, in posterior view, it is much wider than long (Fig. 612). The palpus has the embolus loop on "top" of the bulb toward the cymbium (Fig. 616), unlike that of any other *Alpaida.*

Paratypes. COLOMBIA *Valle*: Cali, 1,000 m, 1976, ♂; Río Jamundí near Jamundí, 1,000 m, 9 Dec. 1969, ♂, 17 June 1970, ♂ (all W. Eberhard, MCZ).

Alpaida nonoai new species
Figures 617–622; Map 5

Holotype. Female from Parque Estadual de Nonoai, Nonoai, Rio Grande do Sul, Brazil, 13 Jan. 1985 (A. A. Lise, MCN no. 12912). The specific name is a noun in apposition after the locality.

Description. Female. Carapace yellowish white with dusky median patch. Sternum, legs yellowish white. Dorsum of abdomen with three white bands, laterals with scalloped dorsal border, median ones indistinct in outline, and two posterior black patches (Figs. 619, 620); venter yellowish white, with black spinnerets. Anterior lateral eyes the diameter, posterior median eyes 1.6 diameters, posterior lateral eyes 1.3 diameters of anterior median eyes. Anterior median eyes slightly more than one diameter apart, posterior medians about their diameter apart. Abdomen oval. Total length 5.1 mm. Carapace 1.8 mm long, 1.3 wide. First femur 1.7 mm; patella and tibia 1.9; metatarsus 1.1; tarsus 0.7. Second patella and tibia 1.5 mm; third 1.0; fourth 1.6.

Male. Coloration as in female but with more black pigment on dorsum of abdomen (Fig. 621). Total length 3.9 mm. Carapace 1.8 mm long, 1.5 wide. First femur 1.8 mm; patella and tibia 2.1; metatarsus 1.1; tarsus 0.5. Second patella and tibia 1.8 mm; third 1.1; fourth 1.7.

Variation. Total length of females from 3.8 to 5.5 mm, males from 3.5 to 4.0. The abdomen of some specimens is oval (Fig. 619), of others, elongate (Fig. 620).

The female holotype and a male from Rio Grande do Sul (MCN) are described and illustrated.

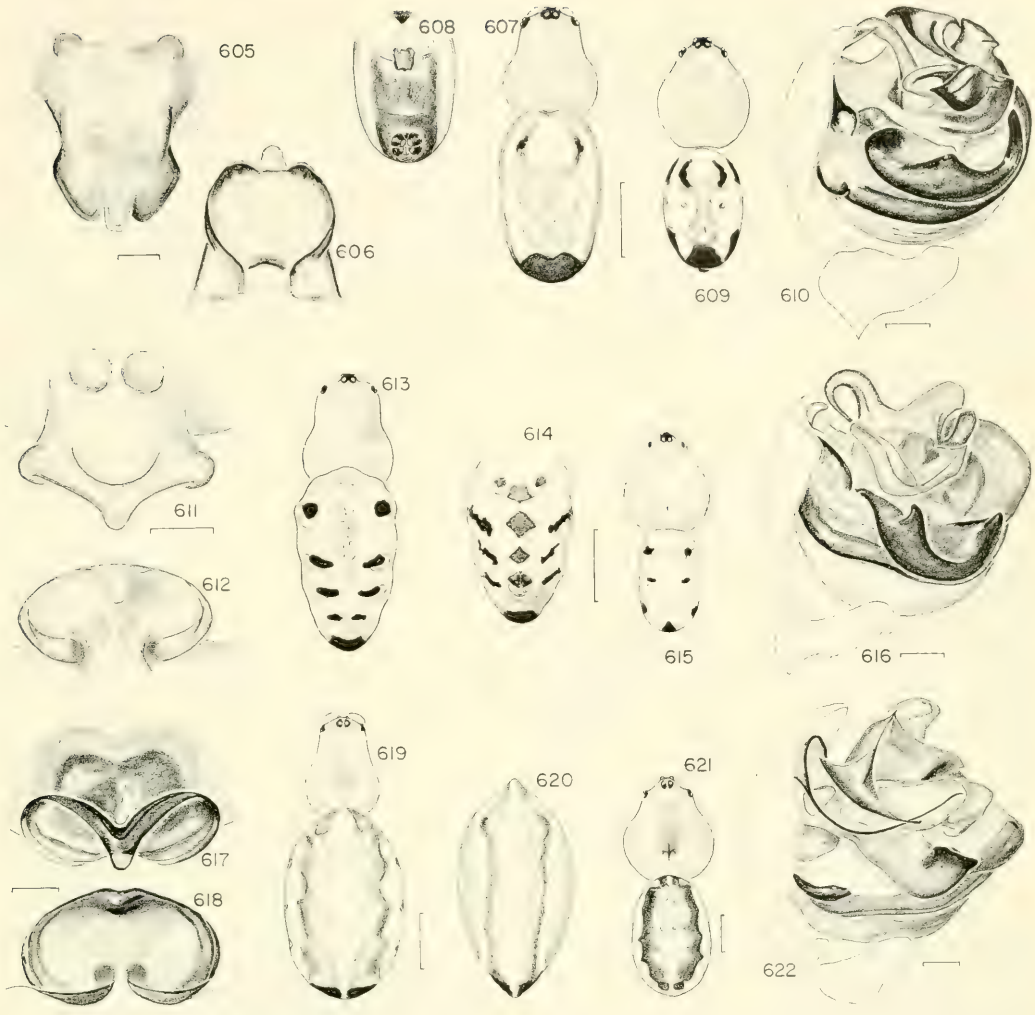
Diagnosis. Females distinguished from similar species by the epigynum: in ventral view, the median plate shows as a bulge on each side of the lip (Fig. 617, as in *A. leucogramma*), and in posterior view, the median plate is convex (Fig. 618), distinct from *A. leucogramma.* The male distinguished from most *Alpaida* by the long filamentous embolus, which lies across the middle of the bulb, by a flat keel on the distal end of the median apophysis and by lobed terminal apophysis (Fig. 622).

Paratypes. BRAZIL *São Paulo*: Boracéia, 28 Feb. 1967, ♀ (P. de Biasi, MZSP 6122); São Paulo, 21 Dec. 1945, ♂ (H. Sick, AMNH). *Rio Grande do Sul*: São Jacó, Arroio do Meio, 9 Jan. 1985, ♀ (A. A. Lise, MCN); Montenegro, 6 Oct. 1977, 8♂, ♀ (A. A. Lise, H. E. Buckup, MCN); Rio Pardo, 15 Dec. 1976, ♂ (F. R. Mayer, MCN); Triunfo, 20 Oct. 1977, 4♀, 2♂ (E. H. Buckup, MCN), 28 Nov. 1977, 2♀, ♂ (H. Bischoff, MCN 7333); Três Coroas, 15 Dec. 1976, ♀ (E. H. Buckup 4932, MCN); Canela, 3 Feb. 1967, ♀ (A. A. Lise, MCN), 31 Dec. 1973, ♀ (A. A. Lise, MCN 2055); Vila Oliva, Caxias do Sul, 5 Jan. 1976, ♀ (P. A. Buckup, MCN 3697); Parque Estadual de Nonoai, Nonoai, 14 Jan. 1985, ♀ (A. A. Lise, MCN 12810); Igrejinha, Jaquara, 19 Oct. 1967, 3♀, 3♂ (P. de Biasi, MZSP 7154).

Alpaida marta new species
Figures 623–627; Map 5

Holotype. Female from Sierra Nevada de Santa Marta, San Pedro, 1,200 m, Dpto. Magdalena, Colombia, 3 May 1975 (J. Kochalka, MCZ). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, sternum, legs yellowish white. Dorsum of abdomen with four pairs of black spots, one on each protuberance, and a pair of larger black spots posteriorly with reddish longitudinal streaks broken by greenish areas (Fig. 625); venter yellowish without marks, spinnerets dusky. Posterior median eyes 1.4 diameters of anterior medians; laterals subequal to anterior medians. Anterior median eyes 1.5 their diameters apart; posterior median eyes slightly more than their diameter apart. Abdomen pointed ante-



Figures 605–610. *Alpaida silencio* n. sp. 605–607, female. 605, epigynum, ventral. 606, epigynum, posterior. 607, dorsal. 608, ventral. 609, 610, male. 609, dorsal. 610, left palpus.

Figures 611–616. *A. cali* n. sp. 611–614, female. 611, epigynum, ventral. 612, epigynum, posterior. 613, dorsal. 614, ventral. 615, 616, male. 615, dorsal. 616, ventral.

Figures 617–622. *A. nonoai* n. sp. 617–620, female. 617, epigynum, ventral. 618, epigynum, posterior. 619, 620, dorsal. 621, 622, male. 621, dorsal. 622, palpus.

Scale lines. 1.0 mm; genitalia, 0.1 mm.

riorly and posteriorly with four pairs of small lateral humps (Fig. 625). Total length 5.2 mm. Carapace 1.9 mm long, 1.5 wide. First femur 2.1 mm; patella and tibia 2.4; metatarsus 1.7; tarsus 0.7. Second patella and tibia 2.0 mm; third 1.2; fourth 1.9.

Male. Carapace coloration delicate, reddish and green. Sternum orange. Legs green. Dorsum of abdomen with two red bands separated by green, green sides and black spots (Fig. 626); venter reddish. Eyes as in female. Second tibiae thicker than first with macrosetae. Total length 4.0 mm. Carapace 2.0 mm long, 1.3 wide. First fe-

mur 1.9 mm; patella and tibia 2.4; metatarsus 1.5; tarsus 0.7. Second patella and tibia 1.7 mm; third 1.1; fourth 1.8.

Diagnosis. The female is distinguished from *A. chickeringi* by the lack of tiny spines on the abdomen (Fig. 625) and from other species by the triangular epigynum in ventral view (Fig. 623) and by the divided median plate in posterior view (Fig. 624). The male differs from *A. chickeringi* by having only one palpal patellar macroseta and having a long filamentous embolus originating from the "top" of the bulb (Fig. 627).

Natural History. The species has been collected in low vegetation.

Paratypes. COLOMBIA *Magdalena*, Sierra Nevada de Santa Marta: W of Cerro Lagila, 1,120 m, 21 April 1975, ♂ (J. Kochalka, MCZ); Serra Nueva Granada, 1,615 m, 7 April 1975, 2♀, imm. (J. Kochalka, MCZ, MNHNP); San Pedro, 1,250 m, 2 Feb. 1974, ♀; above Minca Valley, 880 m, 24 Feb. 1974, ♂ (both J. Kochalka, AMNH).

Alpaida chickeringi new species
Figures 628–634; Map 5

Holotype. Female from Barro Colorado Island, Gatun Lake, Prov. Panamá, Panama, June 1936 (A. M. Chickering, MCZ). The species is named after the collector.

Description. Female. Carapace, sternum, legs yellowish. Dorsum of abdomen yellowish-white; venter with white pigment behind epigynum and around spinnerets (Fig. 632). Legs with some long macrosetae. Abdomen with pairs of humps crowned by spines (Figs. 630, 631). Total length 6.4 mm. Carapace 2.8 mm long, 2.1 wide. First femur 3.1 mm; patella and tibia 3.5; metatarsus 2.4; tarsus 1.1. Second patella and tibia 2.8 mm; third 1.9; fourth 3.2.

Male. Coloration as in female. Legs with long, black macrosetae. Abdomen with paired humps, none pointed (Fig. 633). Total length 5.5 mm. Carapace 2.5 mm long, 2.0 wide. First femur 2.7 mm; patella and tibia 3.1; metatarsus 2.2; tarsus 1.1. Second patella and tibia 2.3 mm; third 1.8; fourth 2.8.

Note. The pigment distribution on the venter makes it possible to match male and female. The holotype female has a growth injury in the head region and has only five eyes.

Variation. Females vary in total length from 6.4 to 7.4 mm, males from 4.5 to 6.1 mm.

The female holotype and a male from the type locality are described and illustrated.

Diagnosis. The female is distinguished from most *Alpaida* by the tiny pairs of spines on the abdomen and from *A. almada* and *A. sulphurea* by the epigynum, which has a swollen triangular area just anterior to the median lobe (Fig. 628). The male is distinguished from most others by the two macrosetae on the palpal patella and from *A. almada* by the sword-shaped embolus hanging from the "top" of the bulb, almost parallel to the cymbium (Fig. 634).

Paratypes. PANAMA *Panamá*: Barro Colorado Isl., Lago Gatún, Aug. 1936, ♂

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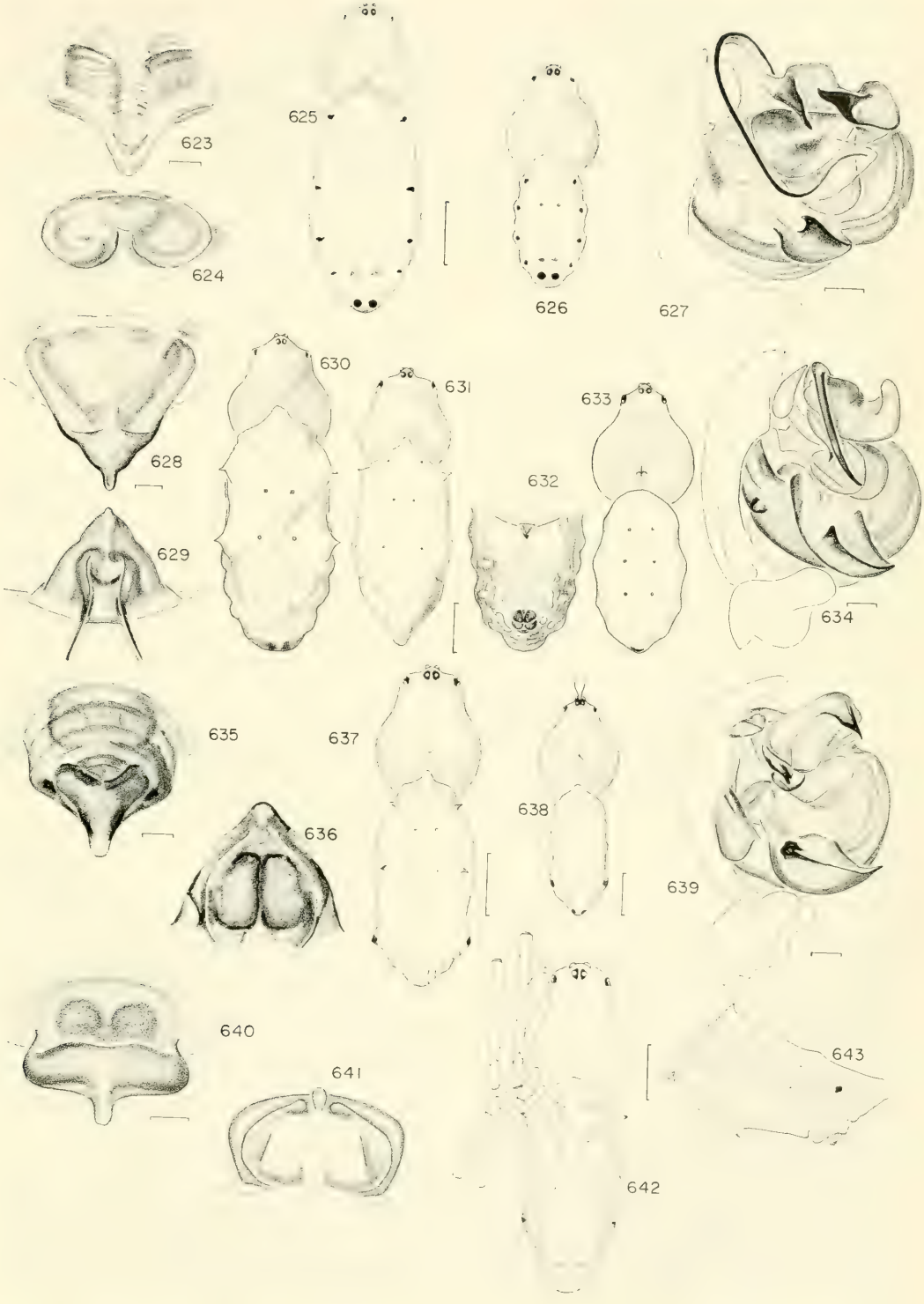
Figures 623–627. *Alpaida marta* n. sp. 623–625, female. 623, epigynum, ventral. 624, epigynum, posterior. 625, dorsal. 626, 627, male. 626, dorsal. 627, left palpus.

Figures 628–634. *A. chickeringi* n. sp. 628–632, female. 628, epigynum, ventral. 629, epigynum, posterior. 630, 631, dorsal. 632, ventral. 633, 634, male. 633, dorsal. 634, palpus.

Figures 635–639. *A. almada* n. sp. 635–637, female. 635, epigynum, ventral. 636, epigynum, posterior. 637, dorsal. 638, 639, male. 638, dorsal. 639, palpus.

Figures 640–643. *A. sulphurea* (Taczanowski), female. 640, epigynum, ventral. 641, epigynum, posterior. 642, dorsal. 643, lateral.

Scale lines. 1.0 mm; genitalia, 0.1 mm.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(A. M. Chickering, MCZ); June 1950, ♀ (Zetek, MCZ); Forest Reserve, Aug. 1936, ♂ (Zetek, MCZ). LESSER ANTILLES *Trinidad*: Simla, 12 Dec. 1954, ♂ (A. M. Nadler, AMNH). GUYANA *Bartica Distr.*: Kartabo, 1928, ♂, ♀ (AMNH). COLOMBIA *Nariño*: La Planada, 1,800 m, 7 km S Choconés, nr. Ricaurte, July 1986, ♂ (W. Eberhard, MCZ). BRAZIL *Mato Grosso*: 260 km N Xavantina, 400 m, Feb.–Apr. 1969, ♂ (Xavant.-Chachimbo Exp., MCZ).

Alpaida almada new species
Figures 635–639; Map 5

Holotype. Female from Fazenda Almada, Uruçuca, Bahia, Brazil, 27 Nov. 1977 (J. S. Santos, MCN no. 10492). The specific name is a noun in apposition after the type locality.

Description. Female. Carapace, sternum, legs yellow. Dorsum and sides of abdomen white, small black spot on posterior lateral humps (Fig. 637); venter without pigment except for a pair of white patches behind genital groove. Anterior median eyes one diameter apart, posterior median eyes 1.5 diameters apart. Legs with many macrosetae and smaller setae. Abdomen with two pairs of lateral thorns, a posterior pair of lateral humps, and an anterior median hump; posterior with some setae (Fig. 637). Total length 6.8 mm. Carapace 2.7 mm long, 2.2 wide. First femur 3.1 mm; patella and tibia 3.7; metatarsus 2.8; tarsus 1.2. Second patella and tibia 3.1 mm; third 2.0; fourth 3.4.

Male. Coloration as in female, except sides of abdomen with little white pigment (Fig. 638). Carapace with two long macrosetae from between median ocular quadrangle. Anterior median eyes and posterior median eyes each slightly more than their diameters apart. Legs with many long macrosetae. Total length 5.5 mm. Carapace 2.7 mm long, 1.9 wide. First femur 2.7 mm; patella and tibia 3.1; metatarsus 2.0; tarsus 1.1. Second patella and tibia 2.3 mm; third 1.8; fourth 3.1.

Note. The male's right palpus has embolus tip covered by part of conductor, perhaps a piece that breaks off when mating.

Diagnosis. The female is distinguished from *A. chickeringi* in posterior view of the epigynum by two large seminal receptacles visible through a wide transparent median plate (Fig. 636). The male, like *A. chickeringi* and unlike most species, has two patellar setae on the palpal patella; unlike *A. chickeringi*, the palpus has a short embolus and a large terminal apophysis ending in a distal hood (Fig. 639).

Paratypes. BRAZIL *Bahia*: Fazenda Almada, Uruçuca, 27 Nov. 1977, ♀ (J. S. Santos, MCN 10163), 26 Nov. 1977, ♂ (J. S. Santos, MCN 10344).

Alpaida sulphurea (Taczanowski), new combination
Figures 640–643; Map 5

Nephila sulphurea Taczanowski 1873: 148. Female holotype from Cayenne, French Guiana (PAN), examined.

Note. Bonnet (1958) and Roewer (1942) consider this name a synonym of *Nephila clavipes*.

Description. Female. Carapace, sternum, legs, yellow-white. Dorsum of abdomen white, sides with white spots and some black spots inside the white (Fig. 642); venter without pigment. Anterior median eyes less than their diameter apart, posterior medians a little more than their diameter apart. Abdomen longer than wide, with an anterior lateral spine on each side (Fig. 642). Total length 5.5 mm. Carapace 2.0 mm long, 1.5 wide. First femur 2.3 mm; patella and tibia 2.9; metatarsus 2.0; tarsus 0.9. Second patella and tibia 2.3 mm; third 1.4; fourth 2.4.

Note. This species must have been yellow when Taczanowski named it.

Diagnosis. This female is distinguished from *A. chickeringi* and *A. almada* by the long transverse lip on the epigynum (Fig. 640).

LITERATURE CITED

ARCHER, A. F. 1951. Studies in the orbweaving spiders (Argiopidae). I. American Museum Novitates, no. **1487:** 1–52.

———. 1966. Nuevos argiopidos de las Antillas. Caribbean Journal of Science, **5:** 129–133.

———. 1971. Especies nuevas de Argiopidos peruanos. Revista peruana de entomologia agricola, **14:** 157–159.

BADCOCK, H. D. 1932. Reports of an expedition to Paraguay and Brazil in 1926–1927 supported by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for the Universities of Scotland. Arachnida from the Paraguayan Chaco. Journal of the Linnaean Society of London, **38:** 1–48.

BERTKAU, P. 1880. Verzeichniss der von Prof. Ed. van Beneden auf seiner im Auftrage der Belgischen Regierung unternommen wissenschaftlicher Reise nach Brasilien und La Plata im Jahren 1872–1873 gesammelten Arachniden. Memoires couronnés et memoires des savants étrangers, publiés par l'Académie royale des sciences, des lettres et des beaux-arts de Belgique, **43:** 1–20.

BLACKWALL, J. 1863. Description of newly discovered spiders captured in Rio de Janeiro by John Gray and The Rev. Hamlet Clark. The Annals and Magazines of Natural History, **3**(11): 29–45.

BONNET, P. 1955. Bibliographia araneorum, Toulouse, **2**(1): 1–918.

———. 1956. Bibliographia araneorum, Toulouse, **2**(2): 919–1926.

———. 1958. Bibliographia araneorum, Toulouse, **2**(4): 3027–4230.

BRIGNOLI, P. M. 1983. A catalogue of the Araneae described between 1940 and 1981. Manchester Univ. Press, Manchester, 755 pp.

CAMBRIDGE, F. PICKARD-. 1904. Arachnida, Araneidea. **1:** 1–56. *In* Biologia Centrali-Americana Zoologia, London.

CAMBRIDGE, O. PICKARD-. 1889. Arachnida, Araneidea. **1:** 1–56. *In* Biologia Centrali-Americana Zoologia, London.

———. 1893. Arachnida, Araneidea. **1:** 105–120. *In* Biologia Centrali-Americana Zoologia, London.

CAPORIACCO, L. DI. 1947. Diagnosi preliminari delle specie di aracnidi della Guiana Brittanica raccolte da Beccari e Romiti. Monitore zoologico italiano, **56:** 20–34.

———. 1948. Arachnida of British Guiana collected by Prof. Beccari. Proceedings of the Zoological Society of London, **118:** 607–747.

———. 1954. Araignées de la Guyane Française du Muséum d'Histoire Naturelle de Paris. Commentationes Pontificia Academia Scientiarum, **16:** 45–193.

CHAMBERLIN, R. V. 1916. Results of the Yale Peruvian Expedition of 1911. The Arachnida. Bulletin of the Museum of Comparative Zoology, Harvard University, **60**(6): 177–299.

———, AND W. IVIE. 1936. New spiders from Mexico and Panama. Bulletin of the University of Utah, **27**(5): 1–103.

EBERHARD, W. G. 1986. Effects of orb-web geometry on prey interception and retention, pp. 70–100. *In* W. A. Shear (ed.), Spiders. Webs, Behavior and Evolution. Stanford Univ., Press, Stanford, viii + 492 pp.

FABRICIUS, J. C. 1793. Entomologia Systematica emendata et aucta, secundum classes, ordines, genera, species adjectis synonimis, locis observationibus descriptionibus. Hafniae, **2:** 407–428.

KARSCH, F. 1886. Araneologisches aus Südamerika. Berliner entomologische Zeitschrift, **30:** 92–94.

KEYSERLING, E. 1864. Beschreibungen neuer und wenig bekannter Arten aus der Familie Orbitelae Latr. oder Epeiridae Sund. Sitzungsberichte und Abhandlungen der naturwissenschaftlichen Gesellschaft Isis in Dresden, **1863:** 63–98, 119–154.

———. 1865. Beiträge zur Kenntniss der Orbitelae Latrl. Verhandlungen der Kaiserlichen-Königlichen Zoologisch-botanischen Gesellschaft in Wien, **15:** 799–856.

———. 1877. Einige Spinnen von Madagascar. Verhandlungen der Kaiserlichen-Königlichen Zoologisch-botanischen Gesellschaft in Wien, **15:** 799–856.

———. 1878. Spinnen aus Uruguay und einigen anderen Gegenden Amerikas. Verhandlungen der Kaiserlichen-Königlichen Zoologisch-botanischen Gesellschaft in Wien, **27:** 571–624.

———. 1880. Neue Spinnen aus Amerika. Verhandlungen der Kaiserlichen-Königlichen Zoologish-botanischen Gesellschaft in Wien, **29:** 293–349.

———. 1892. Die Spinnen Amerikas. Epeiridae, Nürnberg, **4**(1): 1–208.

———. 1893. Die Spinnen Amerikas. Epeiridae, Nürnberg, **4**(2): 209–377.

KOCH, C. L. 1845. Die Arachniden. Nürnberg. Vol. 11, 174 pp.

LEVI, H. W. 1973. Small orb-weavers of the genus *Araneus* North of Mexico (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, Harvard University, **145:** 473–552.

———. 1976. The orb-weaving genera *Verrucosa*, *Acanthepeira*, *Wagneriana*, *Acacesia*, *Wixia*, *Scoloderus* and *Alpaida* north of Mexico. Bulletin of the Museum of Comparative Zoology, Harvard University, **147:** 351–391.

———. 1985. The spiny orb-weaver genera *Micrathena* and *Chaetacis* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, Harvard University, **150:** 429–618.

———. 1986. The neotropical orb-weaver genera *Chrysometa* and *Homalometa* (Araneae: Tetragnathidae). Bulletin of the Museum of Comparative Zoology, Harvard University, **151:** 91–215.

LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in Herpetology and Ichthyology: Part I. Copeia, 1985 **(3):** 802–832.

LINNEAEUS, C. 1767. Systems Naturae per regna naturae. 12th ed., Stockholm, vol. 1, part 2. pp. 533–1327.

LUBIN, Y. 1978. Seasonal abundance and diversity of web-building spiders in relation to habitat

structure on Barro Colorado Island, Panama. Journal of Arachnology, **6:** 31–51.

McCook, H. C. 1894. American spiders and their spinningwork. Academy of Natural Sciences, Philadelphia, **3:** 1–285.

Mello-Leitão, C. F. de. 1933. Catalogo des Aranhas argentinas. Archivos da escola superior de agricultura e medicina veterinaria, **10**(1): 3–63.

———. 1940. Aranhas do Espirito Santo Coligidas per M. Rosa. Archivos de Zoologia São Paulo, **2**(5): 199–214.

——— 1941a. Catalogo des aranhas de Colombia. Anais da Academia Brasileira de Ciencias, **13:** 233–300.

———. 1941b. Arañas de la provincia de Santa Fé coligidas por el Prof. Biraben. Revista del Museo de La Plata, (nueva serie) Sección Zoología, **2:** 199–225.

———. 1942. Arañas del Chaco y Santiago del Estero. Revista del Museo de La Plata, (nueva serie) Sección Zoología, **2:** 381–426.

———. 1945. Arañas de Misiones, Corrientes y Entre Rios. Revista del Museo de La Plata, (nueva serie) Sección Zoología, **4:** 213–302.

Roewer, C. F. 1942. Katalog de Araneae, Bremen, Vol. 1, pp. 1040.

Schenkel, E. 1953. Bericht über einige Spinnentiere aus Venezuela. Verhandlungen der naturforschenden Gesellschaft in Basel, **64:** 1–57.

Shelly, T. E. 1983. Prey selection by the neotropical spider *Alpaida tuonabo* with notes on web site tenacity. Psyche, **90:** 123–133.

Simon, E. 1895. Histoire naturelle des Araignées. Paris **1**(4): 761–1084.

———.1897a. On the spiders of the Island of St. Vincent. Part IV. Proceedings of the Zoological Society of London, **1897:** 860–890.

———. 1897b. Etudes arachnologiques. 27e Mémoire XIII. Descriptions d'espèces nouvelles de l'ordre des Araneae. Annales de la Societé entomologique de France, **65:** 465–510.

———. 1897c. Liste des Arachnides recueillis aux îles du Cap-Vert dans La République Argentine et le Paraguay et descriptions d'espèces nouvelles. *In* Viaggio del Dott. A. Borelli nella Republica Argentina e nel Paraguay. Bollettino dei Musei di zoologia e di anatomia comparata della Università di Torino, **12**(270): 1–8.

Strand, E. 1908. Diagnosen neuer aussereuropäischer Argiopiden. Zoologischer Anzeiger, **33:** 1–4.

———. 1915. Systematisch-faunistische Studien über paläarktische, afrikanische und amerikanische Spinnen des senckenbergischen Museums. Archiv für Naturgeschichte, **81:** 1–153.

Taczanowski, L. 1872. Les Aranéides de la Guyane française. Horae Societatis Entomologicae Rossicae, **8:** 32–132.

———. 1873. Les Aranéides de la Guyane française. Horae Societatis Entomologicae Rossicae, **9:** 64–150.

———. 1878. Les Aranéides du Pérou Central. Horae Societatis Entomologicae Rossicae, **14:** 140–175.

Tullgren, A. 1905. Araneida from the Swedish Expedition through the Gran Chaco and the Cordilleras. Arkiv för Zoologi, **2**(19): 1–81.

Valle, C. and M. T. Valle. 1972. Algumas observaôes sôbre biologia de Metazygia unguiformis (Keys., 1892). Revista brasileira, Biologia, **32:** (1): 33–40.

Walckenaer, C. A. 1841. Histoire naturelle des Insectes Aptères, Paris, **2:** 1–549.

White, A. 1841. Description of new and little known Arachnida. The Annals and Magazine of Natural History, **1**(7): 471–477.

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